The population dynamics of a riparian spider: interactive effects of flow-related disturbance on cross-ecosystem subsidies and spider habitat

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Contents

Abstract

The transfer of prey resources between ecosystems can have dramatic consequences for both recipient and donor systems by altering food web stability and the likelihood of trophic effects cascading across the ecosystem boundary. Landscape-scale factors influence the importance, direction and magnitude of energy flows, but may also alter the ability of consumer organisms to respond to spatio-temporal changes in allochthonous prey availability. Here, I used flood and drying disturbance gradients to investigate interactions between these two processes on populations of a riparian fishing spider *Dolomedes aquaticus* (Pisauridae).

The abundance of aquatic insects with a winged adult stage, a major component of the diet of *D. aquaticus*, was markedly higher at less flood-prone rivers and declined with increasing flood disturbance. It was expected that spider populations would be largest at these stable rivers where the aquatic prey abundance was highest. However, a habitat (loose, unembedded riverbank rocks) manipulation revealed that the lack of scouring floods at these sites led to habitat-limited populations, preventing response to the increased prey resource. In fact a peak shaped relationship of spider biomass and abundance was found, with the largest spider populations at intermediately disturbed rivers. In addition, patchy habitat availability was the most likely cause of the small scale (4 m^2) aggregation of spiders seen at the most stable and disturbed rivers. These patterns were also associated with strong interactions between the spiders. Stable isotope analysis of field collected spiders and an experimental manipulation of spider densities and food availability indicated that cannibalism rates were likely to be significantly higher at stable and disturbed rivers than those intermediate on the disturbance gradient. Differences in *D. aquaticus* population size structure and life history traits across the flood disturbance gradient were driven by interactions between resource availability, environmental stability and cannibalism rates. To separate the effects of habitat availability and aquatic prey abundance I used drying rivers, as the amount of aquatic insect prey alters as the water recedes. Desiccation mortality and low aquatic prey biomass most likely caused the spiders' spatial distribution and size class structure to alter in drying river reaches, potentially also leading to differences in cannibalism rates.

Overall, cross-ecosystem transfers of prey had large impacts on the distribution, cannibalism rates and life history traits of *D. aquaticus* but their effects were modified by the nature of the ecosystem boundary. Thus river flow regime controlled the magnitude of the subsidy and its use by a consumer. Hence, cross-ecosystem subsidies will not always lead to larger consumer populations and consumer responses will depend on interactions between large-scale processes.

Big and hairy, very scary....

Boris the Spider, The Who

Chapter 1

General Introduction

The significance of biotic connections between ecosystems has been vividly highlighted in the last 10 years. The transfer of resources across ecosystem boundaries can have marked population and community level effects in both the recipient and donor systems and can lead to trophic cascades that cross ecosystem boundaries (e.g. Polis et al. 1997, Nakano and Murakami 2000, Halaj and Wise 2002, Baxter et al. 2004, Knight et al. 2005). In light of the many anthropogenic impacts on ecosystems, such as global climate change (McCarty 2001), habitat fragmentation (Laurance et al. 2002, Harper et al. 2006) and the introduction of exotic species (Vitousek et al. 1997, Mack et al. 2000), understanding how alterations to the nature of adjacent ecosystems and their boundaries affect the linkages between systems is critical.

There has been considerable research into how large-scale processes control the magnitude and direction of energy flows across ecosystem boundaries (e.g. Polis and Hurd 1996, Ben-David et al. 1998, Anderson and Polis 1999, Hilderbrand et al. 1999, Iwata et al. 2003, Cadenasso et al. 2004, Carpenter et al. 2005, McCann et al. 2005) and several dramatic examples of cross ecosystem energy transfers causing trophic cascades (e.g. Spencer et al. 1991, Nakano et al. 1999, Henschel et al. 2001, Power 2001, Bastow et al. 2002, Halaj and Wise 2002, Murakami and Nakano 2002, Sabo and Power 2002, Baxter et al. 2004, Knight et al. 2005, Rand et al. 2006). However, few studies have empirically investigated the general circumstances in which spatial subsidies are likely to cause such large impacts on recipient communities (but see Polis and Hurd 1995, Nakano and Murakami 2000, Kato et al. 2003). A workshop commissioned in 2006 by the US National Science Foundation to investigate the research "frontiers of ecology" highlighted the importance of expanding ecological research from studying the effects of separate processes to developing a predictive framework by examining context dependent responses and the relative importance of interacting variables across environmental gradients (Agrawal et al. 2007). The application of this idea to cross-ecosystem resource transfers will increase our understanding of the circumstances in which linkages between adjacent ecosystems are particularly strong, and ultimately could allow us to predict outcomes

of change to systems. In this thesis I investigate how the nature of the ecosystem boundary modifies the influence of cross-ecosystem prey subsidies on a consumer population. Specifically, how large-scale factors can control both the magnitude of the subsidy and influence how the consumer responds to it.

To predict when cross-ecosystem subsidies are likely to be important we need to understand not only the large-scale processes which influence their magnitude and direction of flow but also how interactions between these processes are likely to control the responses of recipient consumers. Productivity gradients between adjacent ecosystems, the area of donor habitat and the nature and length of boundary are important factors that influence the magnitude and direction of energy flows (Polis et al. 1997, Iwata et al. 2003, Cadenasso et al. 2004, Witman et al. 2004). For example, the structural nature of ecosystem boundaries impacts the dispersal of many potential prey taxa between the systems; the distance adult aquatic insects travel from a river (Delettre and Morvan 2000) or edge effects on terrestrial fauna in fragmented forest landscapes (Laurance et al. 2002). However, I suspect these structural and ecosystem size changes are also likely to change the suitability of the ecotone as a habitat or foraging area for potential consumers of the resource. Thus, as well as controlling the direction and magnitude of the subsidy these large-scale processes could affect when such energy flows will be important in the recipient system .

Disturbances, such as fires, floods and habitat modification that occur across or create new ecosystem boundaries are model situations for exploring these issues. By changing the physical nature of adjacent ecosystems, disturbances likely alter the magnitude of cross-ecosystem resource flows, as well as the spatial distribution of other critical consumer resources, such as suitable habitat. Specifically, this could lead to changes to the spatial and temporal juxtaposition of suitable habitat patches with areas of high resource availability and alterations to the relative productivities of the adjacent systems. Furthermore, alterations to both the biotic and abiotic nature of the ecotone may also affect life history traits of individuals, which in turn could alter the influence these individuals have within one system and across the ecosystem boundary.

Many riparian spiders depend on emerging aquatic insects for a significant proportion of their diet (Sanzone et al. 2003, Kato et al 2004). Spiders are often also an important component of the riparian food web as they can facilitate energy transfer from stream to riparian ecosystems by consuming aquatic insects and in turn being

consumed by birds, bats and lizards (Jackson and Fisher 1986, Sabo and Power 2002, Iwata et al. 2003). Floods change the nature of the riparian vegetation (Bendix and Hupp 2000), which will have impacts on direction and type of energy flows across boundary (Wiens 2002). Conversely, low flows in rivers are likely to affect the availability of aquatic insects as prey, without altering the vegetation structure of the ecotone dramatically. Thus, I investigate the influence that flood regime and drying disturbance have on populations of a riparian consumer; a fishing spider *Dolomedes aquaticus*, through changes to the abundance of aquatic insects, a major prey source for the spiders, as well as physical changes to the riparian boundary. Specifically, I investigate the consequences of these changes for *D. aquaticus* population abundance and size class structure, their life history traits and the prevalence of strong biotic interactions within the populations.

This thesis has been written as a series of stand alone scientific papers intended for publication. Thus, there is some overlap in the introduction and methods sections however, I have attempted to minimise repetition. Figures and tables are numbered from the beginning within each chapter. Chapter 2 has been submitted to Ecology and is in review.

In Chapter 2 patterns in aquatic insect abundance across the disturbance gradient are investigated and related to patterns in *D. aquaticus* population sizes using a large scale survey. In addition, a habitat manipulation experiment investigates the role of habitat availability associated with the flood disturbance regime in controlling the ability for the spiders to respond numerically to the subsidy. In Chapter 3 this is extended and the combined influences of habitat and prey abundance on *D. aquaticus* spatial distributions and intraguild, especially cannibalistic, interactions are investigated across the disturbance gradient. Surveys, experimental mesocosms and stable isotope analysis are used to investigate these effects. Chapter 4 investigates the influence of the nature of the riparian boundary on modifying the life history responses of *D. aquaticus* to a gradient of aquatic prey biomass. The combined effects of aquatic prey subsidy and habitat availability are attempted to be separated in Chapter 5. In this chapter a drying rivers gradient is used to explore the impacts of changing food availability and desiccation related mortality while habitat is held constant. Chapter 6 summarises and explores my overall findings, placing my research within the context of current ecological knowledge and draws general conclusions on the impact of cross-ecosystem prey subsidies on recipient populations.

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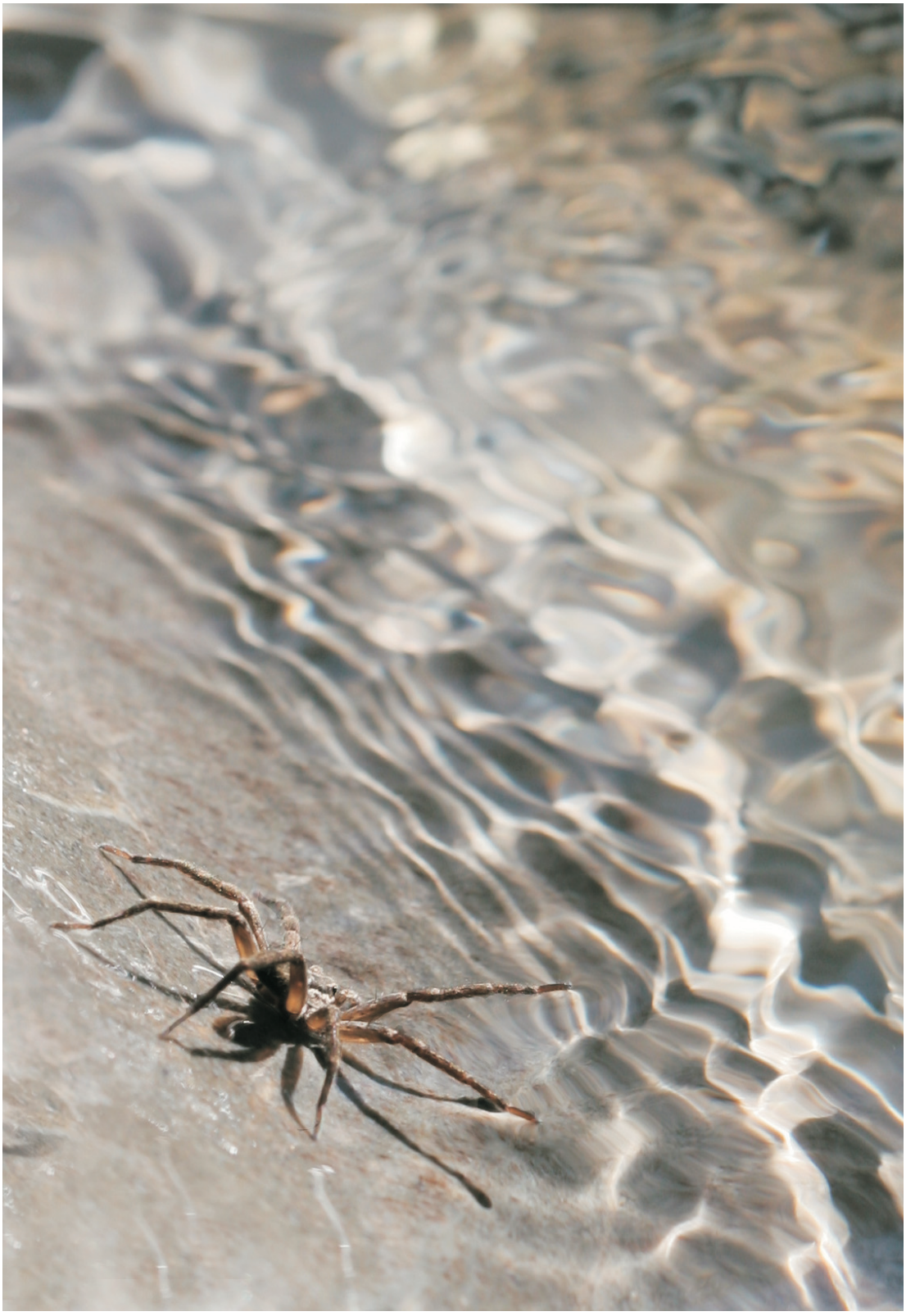

Down came the rain and washed poor incy out...

-incy, wincy spider

Chapter 2

Flooding impacts on responses of a riparian consumer to cross-ecosystem subsidies

This chapter has been submitted to Ecology and is under review. It is presented here in the format in which it was submitted.

ABSTRACT

Landscape-scale processes impact the magnitude and direction of cross-ecosystem resource subsidies but they may also control consumers' numerical and functional responses by altering habitat availability. We investigated effects of the interaction between habitat availability and subsidy level on populations of a riparian fishing spider, *Dolomedes aquaticus*, using a flood disturbance gradient. *D. aquaticus* biomass peaked at rivers with intermediate flood disturbance, rather than at more stable rivers where biomass of aquatic insect prey was markedly higher. Flooding positively influenced spider habitat and an experimental manipulation at stable rivers indicated that unembedded cobbles, preferred *D. aquaticus* habitat, were a limiting factor, preventing response to the increased prey resource at stable sites. Thus landscape-level factors not only controlled the magnitude of resource subsidies but also influenced the ability of consumers to respond to them by altering the physical nature of the ecosystem boundary.

INTRODUCTION

Energy flows across ecosystem boundaries are integral to both recipient and donor ecosystems as they alter the stability of food-webs (Huxel and McCann 1998, Takimoto et al. 2002) and the likelihood that trophic cascades will occur across the boundary (Sabo and Power 2002, Knight et al. 2005). Recent research, stimulated by Polis and colleagues' (1997) review of spatially subsidized food webs, has highlighted the role of landscape-scale factors in influencing the importance, direction and magnitude of energy flows. These factors include differential permeability of

boundaries to energy flux and organism movement (Laurance et al. 2001, Power and Dietrich 2002), boundary shape (Iwata et al. 2003) and boundary length relative to the area of the recipient system (Anderson and Polis 1999), and seasonal differences in productivity between adjacent habitats (Nakano and Murakami 2000). In addition to controlling food-web subsidies, landscape-scale factors such as habitat fragmentation, disturbances or geographic barriers may also limit the ability of consumer organisms to respond numerically or functionally to spatio-temporal changes in allochthonous prey availability by changing the availability of other important resources. Here, we used a flood disturbance gradient to investigate interactions between these two processes on populations of a riparian fishing spider *Dolomedes aquaticus* (Pisauridae) (Goyen 1887).

River size and the nature of the riparian boundary within a riverscape often alter the direction, magnitude and population and community level consequences of energy flow between aquatic and terrestrial ecosystems (Power and Rainey 2000, Iwata et al. 2003, Baxter et al. 2005). Flood disturbances are likely to have pervasive influences on the extent and consequences of aquatic insect subsidies to riparian consumers because they have the potential to reduce the size of aquatic insect populations in addition to altering the suitability of the riparian zone as a habitat (Bell et al. 1999, Ballinger et al. 2005) and foraging ground (e.g. Power and Rainey 2000).

Dolomedes aquaticus is a riparian cursorial spider, which lives among cobbles and boulders on riverbanks throughout New Zealand (Forster and Forster 1999). It is an open riverbank specialist, is largely nocturnal and feeds mainly on aquatic insects (Williams 1979). We expected that, in rivers with unconstrained channels, the flood regime would control the supply of terrestrial and aquatic insect prey as well as influence habitat availability and potentially restrict the ability of spiders to benefit from the aquatic resource subsidy. We hypothesized that at more flood-disturbed rivers the availability of aquatic prey would decline due to the scouring action of spates, however we expected that habitat availability would be high at these sites where cobbles are abundant. At more stable rivers we expected to find high aquatic prey availability but limited spider habitat resources as river banks are more vegetated and exposed cobbles limited. Thus the interaction of habitat and aquatic prey availability at rivers across a flooding disturbance gradient is likely to drive *D. aquaticus* population abundances.

METHODS

The Waimakariri River catchment, South Island, New Zealand, where the study was conducted, is a large braided river subject to frequent and unpredictable flood events at any time of the year, yet within its catchment there are a diverse range of rivers from stable spring-fed systems to frequently disturbed braided rivers. Thirteen rivers spanning the disturbance gradient of this catchment were studied. Generally the riverbanks of all study rivers were largely unvegetated and cobble- or boulder-dominated. Physical characteristics and photographs of the study sites can be found in Appendix I and II, respectively.

Measuring flood disturbance

To measure the timing and intensity of floods we used the painted rock method of Townsend et al. (1997), modified to include grids of rocks in the water and on the bank within 3m of the river edge; a total of 30 rocks at each river. Rock movement was checked monthly between November 2004 and December 2005 and the average proportion of rocks that had moved was calculated as a measure of disturbance. In addition, channel and bank stability was assessed using the river disturbance index (abbreviated here to RDI) (Pfankuch 1975) for the 100m study reach on each river. This index incorporates 15 categories of visually estimated flood-related factors and covers the upper banks, lower banks and the river bottom. The ratings for each category are summed to give an overall index score (32-152) with a higher score indicating a more physically unstable river. Death and Winterbourn (1994) found that Pfankuch river disturbance scores correlated strongly ($r^2 = 0.83$) with a multivariate stability index that included measures of substrate movement, tractive force, variability of depth and current velocity when evaluated on rivers in the same catchment as the present study, including four of the same rivers.

Field survey

Large scale surveys of *D. aquaticus* populations, their habitat and potential aquatic and terrestrial prey were conducted between 26 January and 6 February 2005. A 100 m reach was defined at each river, extending 3 m back from the waters edge on both banks (total 600 m^2). A reach this large reduced the effects of small scale variations in spider abundance associated with habitat patchiness.

D. aquaticus lives under unembedded riverbank rocks within 3 m of the wetted channel edge. To measure the quantity and quality of habitat available to *D. aquaticus* at each river we defined three habitat quality categories based on survey data obtained over the previous year (M. Greenwood, unpublished data). Areas that are too vegetated (>50% coverage) or have few unembedded rocks (< 50 % of rocks unembedded) provide little habitat for spiders and were classified as 'poor'. Banks with less than 50% of the rocks (> 50 mm longest axis, L.A.) embedded in fines provide usable habitat and if vegetation coverage was 5-50 % were classified as 'good'. The presence of riparian vegetation, generally grasses and emergent macrophytes indicated a less flood-prone area which may retain higher terrestrial prey or be important for nest sites. Areas with less than 50% of the rocks (> 50 mm L.A.) embedded in fines and with <5 % vegetation coverage were defined 'intermediate'. Each square metre of the 100 m reach was defined visually as 'good', 'intermediate' or 'poor' and the area of each habitat type was calculated to the nearest square metre for all rivers.

To check our visual differentiation of habitat types we also measured the size (L.A.) and degree of embeddedness of 50 random particles in each of the three habitat types at each river. Depth of embeddedness was calculated by measuring the total height of the rock perpendicular to the ground and how much was buried in fine sediment (<3-4 mm).

At each river twenty 1 m^2 quadrats within each of the three habitat types were searched for *D. aquaticus*. Quadrats per habitat type were stratified with distance from the river edge, with the first 1 m from the river edge searched first. All spiders were digitally photographed on a 2 mm grid and sexed. The wet weight of spiders was calculated from a cephalothorax width (mm): wet weight regression (mg) ($y= 0.024x^{2.69}$, $r^2=0.90$, n= 151, $p<0.001$). *D. aquaticus* abundance and biomass in each habitat type were multiplied by the extent of that habitat type in the 300 m^2 strip along each river bank and summed.

Standing biomass of aquatic invertebrates was calculated to estimate availability of aquatic prey resources. At each river four Surber samples (0.09 m^2, 500 μm mesh) were taken in riffles within 3 m of the river edge and preserved in 90% ethanol. Invertebrates with a winged adult stage (and therefore likely to be available to spiders as prey) were later counted, identified to genus where possible using standard keys (Winterbourn et al. 2000), oven dried at 60 °C for 48 hours and

weighed in taxonomic groups, generally order. The biomass of potential aquatic prey per 100 m reach was estimated by multiplying mean river width to a maximum of 5 m by the mean dry weight of aquatic insects per square metre. Because the spiders hunt from the river edge they are unlikely to have access to prey over the entire width of the river, hence the restriction to a 5 m width maximum.

To measure terrestrial food availability within the riparian zone five randomly located quadrats (0.25 m^2) within 3 m of the river channel were sampled and the area vacuumed with a portable vacuum cleaner (modified auto vacuum, 12 V, 60 W) in each of the three habitat types. Samples were frozen prior to all invertebrates being counted, identified to order, oven dried at 60° C for 48 hours and weighed to the nearest 0.1 mg.

Habitat manipulation experiment

To determine the influence of habitat availability on the abundance and biomass of *D. aquaticus* we manipulated the bank habitat alongside five stable rivers (≤ 60 on river disturbance index) between 29 December 2004 and 3 January 2005. The purpose of the experiment was to test whether the availability of habitat limited spider numbers at locations where resource subsidies were high. At each river substrate was removed to decrease available habitat, added to increase available habitat, and a control with no change in habitat availability. Treatment units were 10 m long and 2 m wide and were at least 3 m apart with the control treatment in the centre and the other two treatments assigned randomly upstream or downstream. Because insufficient adjacent habitat was present at Cave Stream the control site was sited 30 m upstream of the reduction and addition treatments.

To assess habitat availability we measured the longest axis (L.A.) of 50 randomly selected substratum particles in each treatment area as well as their degree of embeddedness (as described previously) prior to the experimental manipulation. In the decrease treatment all unembedded rocks > 50 mm L.A. were removed and placed loosely on top of the rocks already present in the increase treatment. In this way, available interstitial spaces were effectively doubled in the habitat increase area, bringing the proportion of usable habitat up to a level similar to that found in more disturbed rivers (> 90 on the Pfankuch river disturbance index). In the control treatment all unembedded rocks over 50 mm were picked up and replaced to control for substrate movement effects. All sites were searched for *D. aquaticus* before the

habitat manipulation and individuals were digitally photographed on a 2 mm grid and sexed, before being replaced where they were found. Presence of eggsacs was also recorded. Subsequently spider abundance was measured monthly for four months and again after 14 months using the same method. Substratum size and embeddedness were recorded on all dates except in the second month after the manipulation.

Analyses

To evaluate relationships between the river disturbance index and tracer rock movement as well as aquatic food availability, linear and non-linear regressions, respectively, were performed. Relationships between spider biomass and abundance and the river disturbance index were tested with quadratic regressions. For all analyses rivers were treated as replicates (n=13) and post-hoc Tukey tests were performed where necessary. To test for between-treatment differences in substrate size, substrate embeddedness, spider abundance, spider biomass, and the proportion of large females prior to the experimental habitat manipulation, one-way ANOVAs were used. To evaluate the influence of the habitat manipulation, post-manipulation spider abundance, biomass and habitat characteristics were tested using a repeated measures design with treatment and time as main effects and rivers (n=5) as replicates. Analyses of habitat characteristics used all three treatments, whereas analyses of spider biomass, number and the proportion of collected spiders that were large females used the change in numbers relative to the control at each time to account for seasonal changes in abundances at the different rivers.

Analyses of physical characteristics and the habitat manipulation experiment were performed in Statistica (Statsoft Inc. 2003), whereas those for the spider populations were conducted using R (R Development Core Team 2005). All data were $\log_e (+1)$ transformed when necessary to meet assumptions of normality and heteroscedasticity.

RESULTS

The visually assessed categories of habitat type showed good concordance with measured substrate size and embeddedness. Substrate size was significantly larger in good habitat than in intermediate or poor habitat (one way ANOVA, $F_{2, 12} = 6.21$, $P < 0.01$, Tukey post-hoc test) and the proportion of usable *D. aquaticus* habitat (i.e.,

unembedded rocks > 50 mm) was higher in the good and intermediate habitat categories than in the poor habitat (one-way ANOVA: $F_{2, 12} = 75.46$, $P < 0.001$, Tukey post-hoc test). We found a significant positive linear relationship ($r^2 = 0.85$) between movement of painted tracer rocks over 12 months and the river stability index score (Fig. 1a) indicating that the two methods used to define flood disturbance gave similar results. As the river disturbance index integrates the effects of floods over a longer time period than our rock tracer study, the index was used as a measure of flooding disturbance in all subsequent analyses.

The biomass of benthic insects with a winged adult stage in each river was significantly and positively related to the number of adult aquatic insects caught in the riparian vacuum samples ($F_{1, 12} = 8.99$, $P = 0.012$, $r^2 = 0.45$), indicating that standing biomass of aquatic larvae in these rivers is a good surrogate for the abundance of adult aquatic insects available as potential prey for *D. aquaticus*. Potential terrestrial prey for *D. aquaticus* changed little across the disturbance gradient. However, the standing biomass of aquatic invertebrates, i.e. potential prey for *D. aquaticus*, was highest in the least disturbed rivers and declined sharply in the intermediately or highly disturbed rivers (Fig. 1b). Although, we are likely to have overestimated the biomass of aquatic prey available to *D. aquaticus* as they mainly catch prey emerging on the water surface (Williams 1979), the relative pattern across the disturbance gradient will remain the same.

The proportion of usable spider habitat available showed the opposite pattern (Fig. 1c) with a higher proportion of habitat present in the more disturbed rivers. Stable rivers therefore contained more potential prey than disturbed rivers but less habitat for the spiders. Despite the high abundance of both aquatic and terrestrial spider prey at stable rivers, spider numbers and biomass both peaked at intermediate levels of stability (Fig. 1d, e). *D. aquaticus* was present in very low numbers and biomass in both the most stable and most disturbed rivers but spiders were two to three times more abundant in rivers with intermediate levels of disturbance.

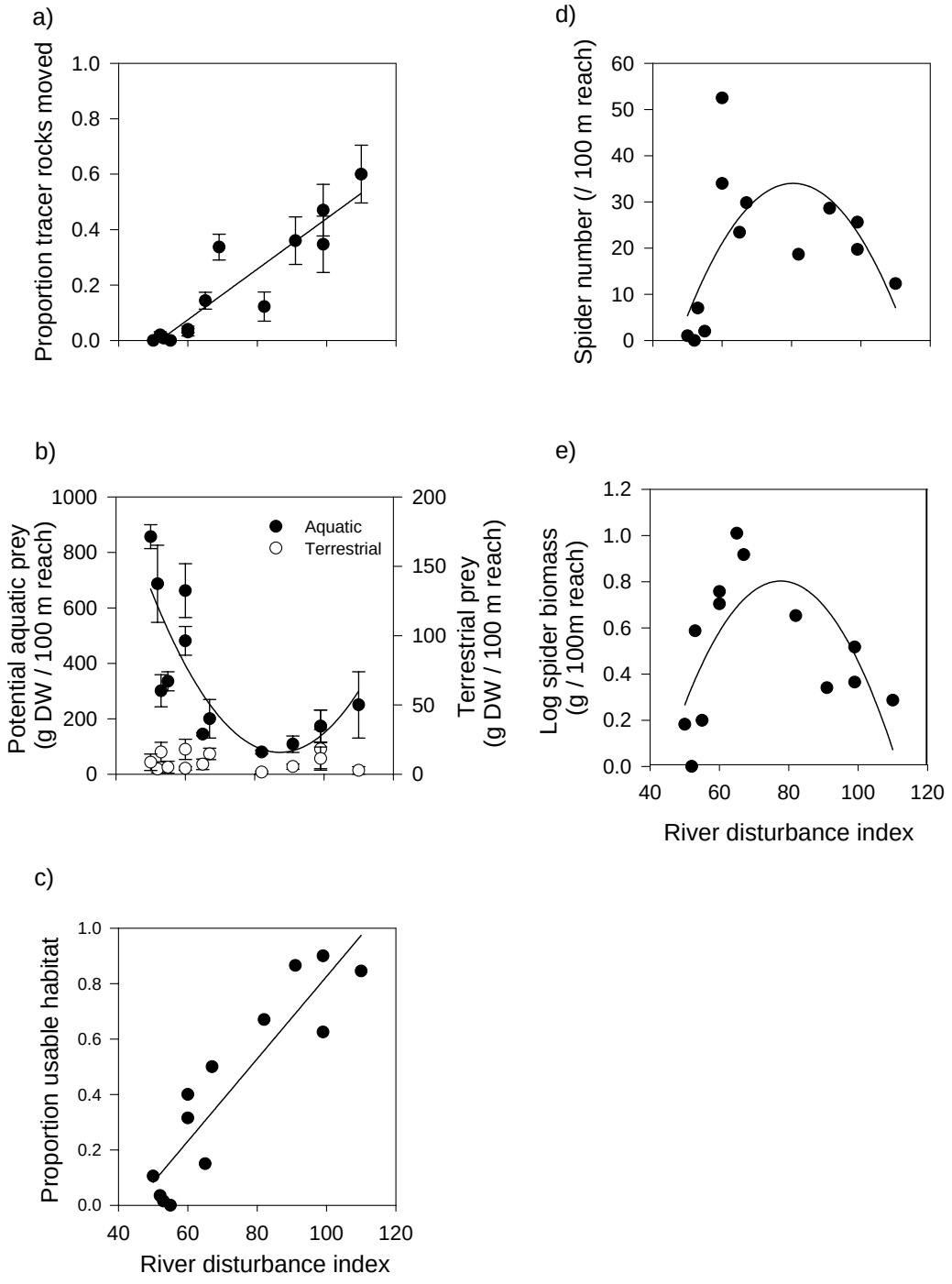

Figure 1 Mean proportion of (a) instream and riverbank tracer rock movement over twelve months ($r^2 = 0.85$, $P_{(0.05,\ 12)} < 0.001$), (b) mean dry weight of potential aquatic (closed circles) and terrestrial (open circles) prey per 100 m reach of river (aquatic: $r^2 = 0.66$, $P_{(0.05,\ 12)} < 0.001$, y= 84.4*x / (-44.8+x)) and (c) the proportion of usable habitat (i.e., loose unembedded rocks) available within 2 m of the river edge over a 100 m reach ($r^2 = 0.83$, $P_{(0.05,\ 12)} = <0.001$). The (d) number ($r^2 = 0.43$, $F_{1,\ 10} = 8.16$, $P_{(0.05,\ 12)} = 0.017$) and (e) biomass ($r^2 = 0.45$, $F_{1,\ 10} = 6.83$, $P_{(0.05,\ 12)} = 0.026$) of *D. aquaticus*, per 100 m reach of river across a flood disturbance gradient measured by the river disturbance index. A high river disturbance index score indicates a river frequently or severely disturbed by floods. Error bars indicate ± 1 SE of river means.

Habitat manipulation experiment

The habitat manipulation experiment directly tested whether habitat availability limited spider abundance, despite the high abundance of food in the stable rivers. Neither substrate size (Fig 2a; $F_{2, 4} = 0.37$, $P = 0.70$) nor the proportion of embedded rocks (Fig 2b; $F_{2, 4} = 1.77$, $P = 0.22$) was significantly different across treatments before the habitat manipulation, however, after the manipulation substrate size increased and embeddedness decreased in the habitat addition areas (Fig 2a & b; substrate size: $F_{2, 9} = 6.74$, $P = 0.02$; embeddedness: $F_{2, 9} = 17.56$, $P = 0.001$). Substrate size also decreased significantly over time after the manipulation ($F_{2, 18} = 3.57$, $P = 0.05$) and substrate embeddedness increased ($F_{2, 18} = 4.42$, $P = 0.03$).

Numbers of spiders did not differ among treatments before the manipulation (treatment: $F_{1, 4} = 0.86$, $P = 0.39$), however, after the manipulation numbers of spiders tended to increase in the addition treatment and decrease in the reduction treatment compared to the control (Fig 2c; treatment: $F_{1, 8} = 3.8$, $P = 0.07$). Spider biomass did not vary between treatments before the manipulation ($F_{1, 4} = 0.07$, $P = 0.80$) but increased in the habitat addition treatment one month after the manipulation and remained higher than the control treatment for 14 months (Fig 2d; $F_{1, 8} = 6.42$, $P = 0.04$).

The proportion of large females (cephalothorax width >8 mm), indicating likely breeding females, did not differ between treatments before the habitat manipulation ($F_{1, 4} = 0.11$, $P = 0.75$) but differed significantly between treatments after the manipulation ($F_{1, 8}$ 23.17, $P = 0.001$). More large females were found where habitat had been added, than in habitat reduction and control treatments and this effect was most marked 14 months after the manipulation (Fig 2e).

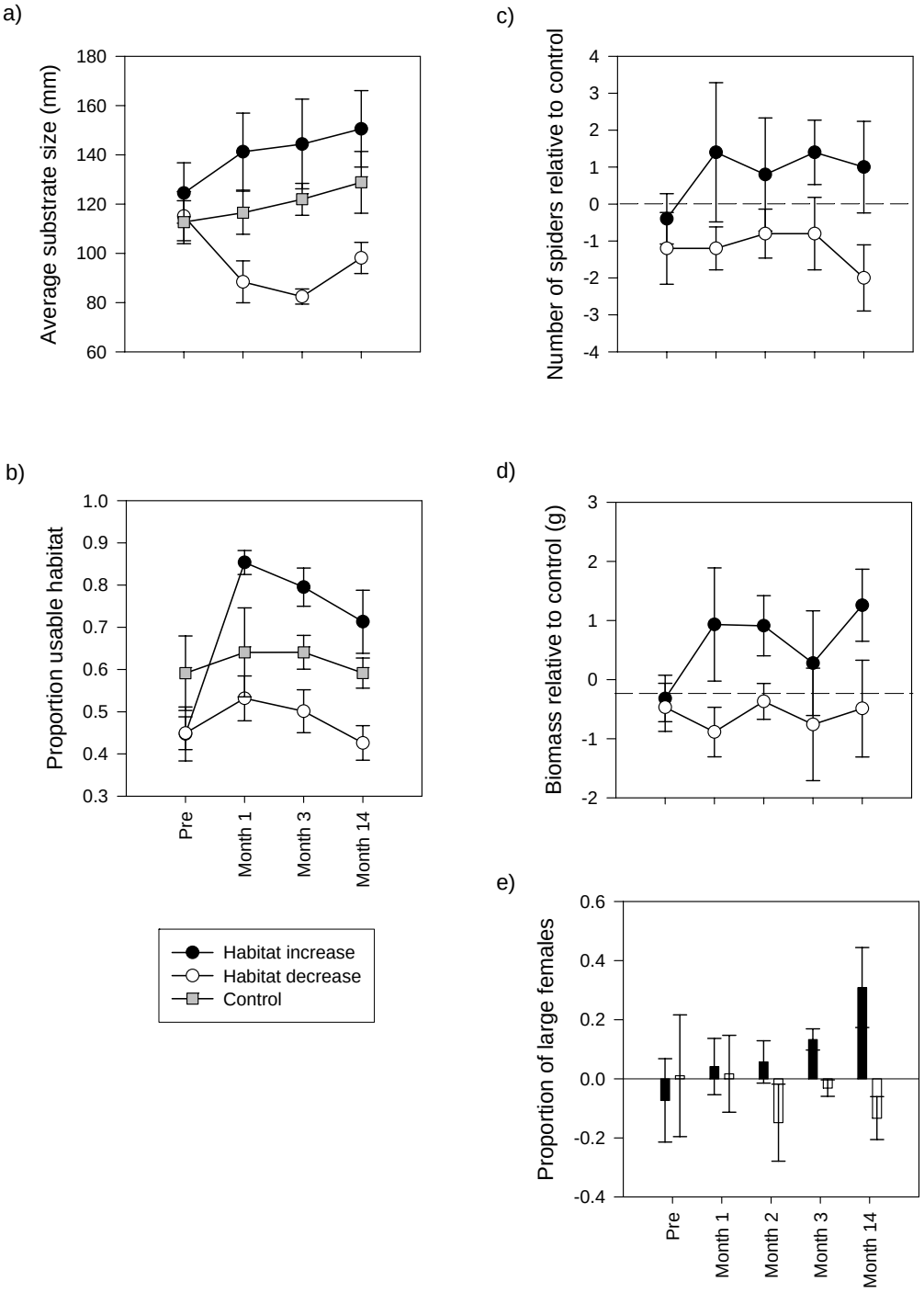

Figure 2 Mean (a) substrate size and (b) proportion of rocks larger than 50 mm embedded more than one fifth of their depth before (pre) the habitat manipulation experiment and one, three and 14 months after the manipulation. Loose, unembedded rocks over 50 mm longest axis were removed from the habitat decrease section and added to the habitat increase section. Controls were unmanipulated. Mean (±1 SE) (c) *D. aquaticus* number, (d) biomass and (e) proportion of spiders that were large females (cephalothorax width >8 mm) before habitat manipulation (pre) and one, two, three, and 14 months after rock habitat addition and reduction, relative to the control area at each river. Rivers are replicates (n=5) and error bars are ±1 SE.

DISCUSSION

Although the influence of some landscape-scale processes on the magnitude and direction of cross-ecosystem subsidies is comparatively well known (e.g. relative productivity, Nakano and Murakami 2000, Cadenasso et al. 2004), few studies have investigated controls on whether subsidies impact consumer populations. This is crucial for understanding and ultimately predicting how cross-ecosystem transfers of energy alter populations and communities.

Our results demonstrate the influence of landscape features on both the magnitude of cross-ecosystem resource subsides and the ability of consumers to utilize those resources by responding numerically. The biomass of winged aquatic insects, which form a high proportion of the diet of many riparian consumers (e.g. Henschel et al. 2001, Akamatsu et al. 2004), was substantially altered by the flooding regime of the rivers studied. In addition, by changing physical habitat characteristics, flood-disturbances impacted the ability of the consumer to respond to the subsidy. The interaction of these two processes, (i.e., the subsidy and habitat availability), which were controlled at landscape-scales, determined the numerical responses of the consumer across the disturbance gradient and resulted in the observed peaked patterns of spider abundance and biomass.

D. aquaticus depend on emerging aquatic insects for a large proportion of their diet (Williams 1979, Collier et al. 2002) and preliminary stable isotope investigations in the rivers studied here suggest 38 to 92 percent aquatic origin (M. Greenwood unpublished data, n=20). Rates of emergence of aerial aquatic insects can be greatly affected by the nature of the riverscape (e.g. Power 1990). In concordance with this we found a higher standing biomass of aquatic larvae with a winged adult stage, indicating a higher abundance of emerging aquatic insects available as prey (Statzner and Resh 1993) to *D. aquaticus*, at stable rivers (RDI $\leq$ 60).

However, as well as influencing the abundance of prey from an adjacent ecosystem the characteristics of the landscape also affect an organism's ability to make use of the resource. In our case the flooding regime of the river also controlled the physical characteristics of the riparian zone, and therefore the quantity and quality of habitat for spiders (Bonn et al. 2002). Like many riparian cursorial spiders (e.g. Sabo and Power 2002), *D. aquaticus* lives under loose unembedded rocks close to the rivers edge. The lack of scouring floods at stable rivers enables a high proportion of

the banks to be vegetated and there are consequently few areas with cobbles unembedded enough to provide habitat for *D. aquaticus*.

When we experimentally increased the amount of habitat (loose, unembedded rocks) at stable rivers in 20 m^2 areas to levels similar to disturbed rivers (from 40% usable habitat pre-manipulation to ~ 80%) the number, biomass and proportion of spiders that were large females (ct width > 8 mm) increased. These effects persisted, and even increased in strength, up to 14 months after the manipulation. At this time the number and biomass of spiders in the habitat addition sites was nearly 100 % greater than that in the control treatment and nearly twice as high as the habitat reduction treatment. Therefore habitat limitation at stable rivers was suppressing population sizes and preventing the spiders from benefiting from the higher amounts of aquatic prey available.

The increase in abundance and biomass of *D. aquaticus* and the higher proportion of large females in the habitat addition sites fourteen months after the manipulation indicates that if habitat is provided the spiders can take advantage of the increased food supply from the aquatic environment and respond numerically. The increase in the number of large females, and the time lag for this increase to occur, suggests that growth or developmental rates may have been influenced by the aquatic subsidy (Kreiter and Wise 2001). In addition, six nests with live young were found fourteen months after the manipulation, four in the habitat addition sites, two in the control sites and none in the habitat reduction areas. The proportion of large females in the habitat addition treatment after 14 months was twice as high as that found at disturbed rivers with similar habitat availability (disturbed river 0.25 ± 0.09, stable river habitat increase 0.53 ± 0.13, n=5 rivers for both).

Mortality from floods or food limitation, or a combination of both, are the most likely factors explaining the low abundance and biomass of *D. aquaticus* found at disturbed rivers. The spiders are well adapted to avoid floods; they build their nests on stable islands that are seldom disturbed and comparable numbers of spiders have been found in the same locality before and immediately after a flood (M Greenwood *personal observation*). Low food availability could also be a significant factor, for example, Kreiter and Wise (2001) found food availability limited the fecundity of a North American fishing spider (*Dolomedes triton* Latreille). However, food availability at intermediately disturbed rivers was as low as that in more disturbed rivers, yet *D. aquaticus* biomass was higher at these sites.

Regardless of the mechanism operating at more flood disturbed rivers, we have shown that landscape level factors can not only influence the level of cross-ecosystem subsidies available to consumers but also can affect the ability of the consumer to respond both functionally and numerically to these variations in allochthonous prey abundance by altering the physical nature of the ecosystem boundary. Thus responses of consumers to such spatial subsidies will vary depending on the propensity and ability of the consumer to utilize the resources as well as its specific habitat requirements. Furthermore, cross-ecosystem subsidies will not always lead to larger consumer populations and consumer responses may be complicated by interactions between landscape-level processes. Responses to energy subsidies are often species specific and influenced by seasonal factors (Nakano and Murakami 2000, Kato et al. 2004) and in addition, habitat requirements are often specific to a taxa. The importance of landscape level effects on the magnitude and importance of cross-ecosystem subsidies of resources has been highlighted but it must also be realized that these landscape-level factors can also impact other resources important to consumers.

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Chapter 3

Interactive effects of cross-ecosystem prey subsidies and habitat availability on intraguild predation rates of a riparian consumer

ABSTRACT

Energy transfers across ecosystem boundaries can have dramatic effects on recipient communities by altering strong biotic interactions like intraguild predation. However, the influence of these cross-ecosystem prey subsidies is likely to be modified by the availability of in-situ consumer resources, e.g. habitat. We investigated intraguild predation rates, particularly cannibalism, of a cursorial, riparian spider across a flood disturbance gradient that altered both the magnitude of the subsidy to the spider (winged aquatic insects) and spider habitat availability (loose riverbank rocks). Spider density was affected by the interaction of prey and habitat availability across the environmental gradient. Both stable isotope analysis of spiders and a mesocosm experiment indicated that relative rates of cannibalism were markedly higher at both ends of the disturbance gradient, where small-scale spider densities were highest. The effects of prey from an adjacent ecosystem on intraguild predation rates of a consumer were modified by the availability of an in-situ resource, consumer habitat. Variations in the strengths of interactions indicate that predicting the outcome of energy flows across ecosystem boundaries depends on the magnitude of the subsidy in relation to in-situ resource availability for recipient consumers.

INTRODUCTION

Flows of energy between adjacent ecosystems can have dramatic consequences for the composition, structure and functioning of communities within both recipient and donor ecosystems (e.g. Polis et al. 1997, Nakano and Murakami 2000, Polis et al. 2004, McCann et al. 2005). Such spatial subsidies can cause trophic cascades that cross ecosystem boundaries (e.g. Nakano et al. 1999, Henschel et al. 2001, Knight et al. 2005) and sometimes have a large influence on the temporal stability of food webs

(e.g. Takimoto et al. 2002, McCann et al. 2005) by altering the occurrence and direction of strong biotic interactions, like intraguild predation. These predatory interactions between guild members can have disproportionately large top-down effects on communities if they alter the identity and abundance of top and intermediate predators (Polis et al. 1989, Polis and Holt 1992). For example, the occurrence and rate of predatory interactions between guild members can alter the stability and size distributions of populations, as well as the composition of communities (Dong and Polis 1992, Hopper et al. 1996, Holt and Polis 1997).

The availability of guild and non-guild prey is one of the most important factors influencing rates of intraguild predation (Polis 1981), so subsidies of prey across ecosystem boundaries to consumers are likely to have large influences on community and population dynamics in the recipient ecosystem. Thus, investigating the effects of variations in allochthonous prey availability on rates of intraguild predation is integral to understanding and ultimately predicting outcomes of biotic interactions between adjacent ecosystems. However, the same large-scale variables that alter the magnitude and availability of a subsidy to a consumer may also change other important resources, thus altering the ability of the consumer to respond both functionally and numerically to the increased prey (Chapter 2). The frequency of predatory interactions between guild members is often density dependent (e.g. Polis 1981, Dong and Polis 1992, Buddle et al. 2003, Eitam et al. 2005) especially if multiple size classes are present (Hopper et al. 1996). Large scale patterns in habitat quality and quantity (Rickers and Scheu 2005) as well as the availability of non-guild prey (Polis 1981) influence the density of predator populations, rates of encounters and hence the frequency of intraguild predation. The distribution of these resources also plays an important role in influencing rates of intraguild predation by altering local-scale population densities. Resources that are spatially or temporally patchy may lead to aggregations of predators and increased encounter rates. Thus, the availability of alternative prey sources and relative densities of predator populations, often determined by a combination of prey and habitat availability, are two of the most important factors controlling rates of intraguild predation, especially cannibalism (Dong and Polis 1992). We used an environmental gradient, which affected both the magnitude of a cross-ecosystem subsidy and the availability of suitable habitat for a consumer in an adjacent ecosystem, to investigate cannibalism rates, a specific case of intraguild predation. We tested how the abundance and spatial distribution of

resources across an environmental gradient determined the local-scale density of a population of predators, and then tested how that influenced rates of intraguild predation, notably cannibalism.

A guild, by definition, is comprised of taxa which use similar resources and often predation between members can be strongest among those with the most resource overlap (Polis et al. 1989). Thus, here we assume that guild members have similar habitat and diet preferences. If we also assume that the relative gradients of non-guild prey and habitat availability are stable for more than one generation of the predatory taxa and that temporal trends in prey availability are similar across the environmental gradient we can predict how variations in habitat and spatial subsidy availability across an environmental gradient will affect intraguild predation rates of a consumer. If the distribution of these two important resources varies across an environmental gradient in synchrony (Fig 1a and b) this should lead to similar predator densities (Fig1c), which in turn could lead to similar encounter and intraguild predation rates across the environmental gradient (See Fig 1 legend for details). However, if the availability of suitable habitat and non-guild prey availability have different relationships across the environmental gradient (Fig 1d and e) then population densities of the predatory taxa will vary across this gradient (Fig 1f), altering rates of encounters and predatory events between guild members. Encounter and intraguild predation rates will change depending on the relative influences of density dependence and prey availability on predator densities (see Fig 1 legend for more details). Across an environmental gradient, a mismatch in resource availability could lead to variations in intraguild predation rates, with predatory events being particularly frequent where the availability of the two resources is most different, leading to aggregations of predators.

Riparian spiders often depend on aquatic insects for a large proportion of their diet (Sanzone et al. 2003, Kato et al. 2004), and intraguild predation and cannibalism are relatively common in cursorial, riparian spiders. Such interactions can regulate densities of certain life stages of spiders (Wagner and Wise 1996) and can often be important foraging strategies (Wise 2006). For some cursorial spiders the most productive rivers for aquatic insects may provide the least suitable habitat. Spiders that depend on loose riverbank rocks (Bell et al. 1999, Ballinger et al. 2005) could be limited by habitat availability at rivers where the subsidy from the aquatic environment is highest, due to the vegetated banks of many stable, productive rivers.

In an earlier study (Chapter 2, Fig 1g and h) we found that the availability of aquatic prey was much lower at more flood-prone rivers than those that were flooded less frequently and/or intensely, and that loose, unembedded rocks, which were important habitat for many small riparian predators, are limiting at sites with the highest aquatic food availability. This mis-match of resources across a flood disturbance gradient provided the ideal situation in which to investigate the role of habitat availability in modifying the effects of cross ecosystem subsidies on intraguild predation rates. We investigated large-scale patterns in habitat and aquatic food availability, as well as the spatial distribution of a New Zealand riparian fishing spider *Dolomedes aquaticus* (Goyen 1887) (Pisauridae), across a flood disturbance gradient and explored how these factors influenced intraguild predation rates, especially cannibalism. We predicted that rates of cannibalism would be driven not only by the magnitude of the aquatic subsidy but also mediated by the amount of suitable habitat available. More specifically, we predicted that cannibalism rates would be density dependent and thus highest where a mis-match between the area of habitat and the availability of allochthonous non-guild prey led to population aggregations.

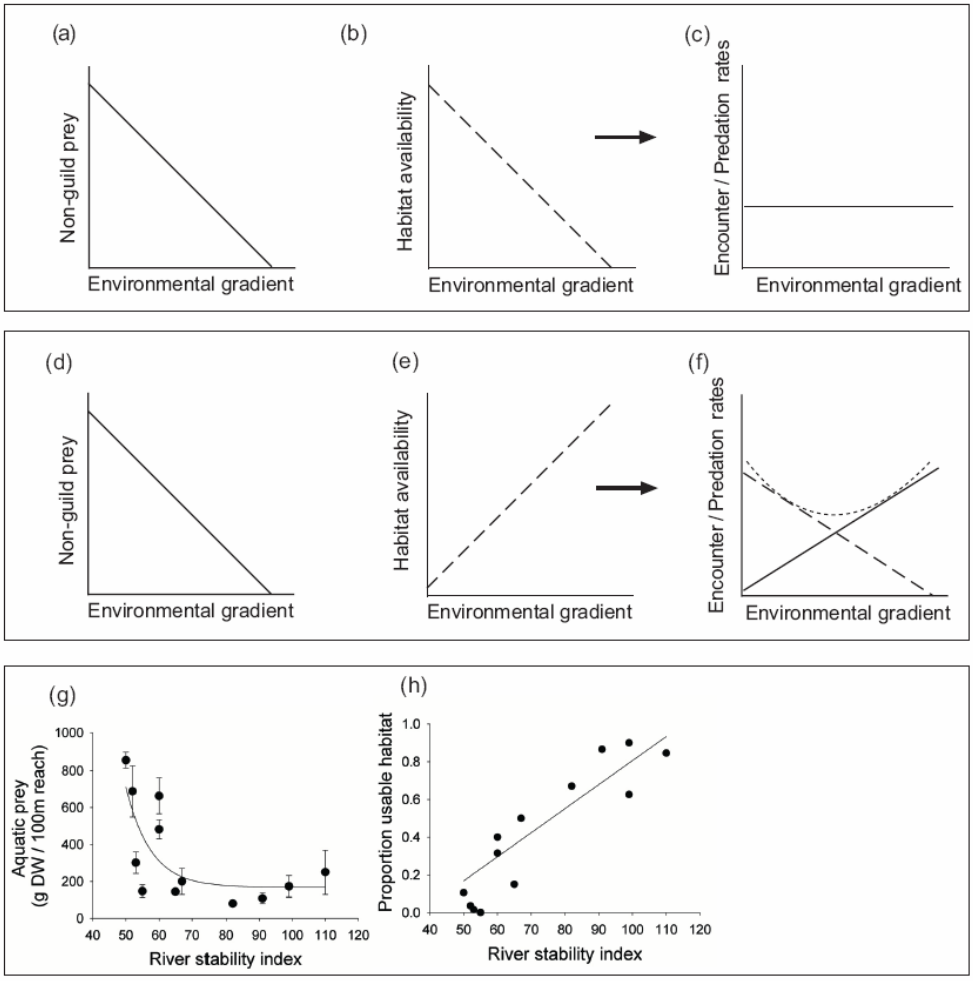

Figure 1 The influence of resource availability on intraguild predation (IGP) rates. If the availability of non-guild prey (a) and quality habitat (b) vary in synchrony across an environmental gradient this should lead to similar predator densities across the gradient (c) assuming per capita non-guild prey consumption by predators is uniform. Similar densities per unit area will lead to similar encounter rates across the environmental gradient and intraguild predation rates will not vary across the gradient if predatory interactions are density dependent. However, if the availability of quality habitat and non-guild prey have different relationships across the environmental gradient (d and e) then population densities of the predatory taxa will vary across this gradient (f), altering rates of encounters and predatory events between guild members. If interactions are density-dependent irrespective of prey availability, then IGP rates should be inversely related to habitat availability (dashed line in f). In addition, if non-guild prey resources are clumped where they are limiting, this could lead to clumped distributions of predatory taxa and high IGP rates (dotted curve in f). However, if the high availability of non-guild prey reduces the propensity for IGP, then IGP rates should be low where habitat is low and non-guild prey availability is high (solid line in f). In our study system mean dry weight of potential aquatic prey per 100 m reach of river decreases ($r^2 = 0.66$, $P_{(0.05,\ 12)} < 0.001$, y= 84.4*x / (-44.8+x)) (g), and the proportion usable habitat (i.e. loose unembedded rocks) available 2 m back from the waters edge over a 100 m reach is enhanced ($r^2 = 0.83$, $P_{(0.05,\ 12)} = <0.001$) (h) across a gradient of increasing flood-related river disturbance (Chapter 2). A high river disturbance index score indicates a river frequently or severely disturbed by floods. Error bars in (g) indicate one SE.

METHODS

Study area

Eleven rivers in the upper Waimakariri River catchment, South Island, New Zealand covering a flood disturbance gradient from stable and spring-fed to a large highly-disturbed, braided river were studied (for detailed study sites descriptions see Appendix I and II). This gradient covers the full flood regime gradient to which *D. aquaticus* spiders are likely to be exposed to in the Canterbury Region of the South Island.

Measuring disturbance

We used the channel disturbance index of Pfankuch (1975) to measure flood-related disturbance. Previously we have demonstrated the river disturbance index is closely related to the movement of tracer rocks over 12 months (r^2 =0.85, Chapter 2), and Death and Winterbourn (1994) also found the index was a useful method of quantifying flood-related disturbance and closely related to other measures. The index incorporates 15 categories of visually estimated flood-related factors, weighted in proportion to their perceived importance, covering three regions of the river channel, upper banks, lower banks and the river bottom. The ratings for each category are summed to give an overall index score for each river, which ranges from 32 to 152 with a high score indicating greater channel instability and by inference greater disturbance by floods.

Dispersion data

We surveyed the spatial distribution of *D. aquaticus* populations at rivers across the disturbance gradient during September 2005. A 60 m reach at each river was divided into 30 adjacent 4 m^2 quadrats along the waters edge. A reach this scale incorporated variations in *D. aquaticus* distributions associated with habitat patches (Chapter 2) while the 4 m^2 quadrats were large enough to ensure multiple spiders could be caught in each. Each quadrat was searched for spiders, which were sexed, digitally photographed on a 2 mm grid to allow size measurements later and released once all searching had been completed for the river. The number of spiders per quadrat was analysed using the standardized Morisita dispersion index (I_p), which is relatively independent of both population density and sample size (Krebs 1998). An I_p of 0

indicates a randomly distributed population while $I_p > 0$ indicates a clumped population (95 % C.I ± 0.5).

Stable isotope analysis

Recent advances in the use of stable isotopes have created a useful tool to aid landscape-scale studies of trophic position and dietary sources. For liquid feeders, like spiders, the inability to perform gut contents analysis limits dietary investigations. In addition, rates of intraguild predation in the field are often based on the density of animals or inferred from ex-situ experiments. Here we used stable isotopes of nitrogen to estimate rates of intraguild predation from field populations across the disturbance gradient.

Trophic position can be estimated from stable nitrogen isotope ratios as consumers become enriched in $\delta^{15}N$ relative to their food (Peterson and Fry 1987, Vander Zanden and Rasmussen 1999) and ratios are comparable across an environmental gradient if they are calculated relative to the $\delta^{15}N$ of an appropriate baseline primary consumer at all sites (Post 2002b). As organisms become more enriched in ^{15}N (relative to ^{14}N) at higher trophic levels, individuals that eat guild members will have higher $\delta^{15}N$ values and hence higher trophic positions than those that do not. Thus, if no differences in food chain length occur below the focal taxa and fractionation is assumed to be similar at sites, stable isotope analysis can be used to estimate rates of intraguild predation, particularly cannibalism (e.g. Rickers et al. 2006) of a species across an environmental gradient. *D. aquaticus* spiders are the top invertebrate predators at the study rivers, so that cannibalistic individuals should be highly enriched in $\delta^{15}N$ (e.g. Hobson and Welch 1995, Harvey et al. 2002).

Samples for stable isotope analysis were collected from eight of the thirteen rivers in January 2005. We collected individuals of a grazing mayfly *Deleatidium* spp. (Leptophlebidae) and crickets (Gryllidae) to use as representative aquatic and terrestrial primary consumers, respectively, to establish basal $\delta^{15}N$ levels. *Deleatidium* spp. and crickets are likely to capture temporal variation in isotope signatures and provide good baseline measures of $\delta^{15}N$ across the disturbance gradient in our system as they were the most common primary consumers across all the study rivers and are likely to have representative diets for their respective ecosystems. To investigate the trophic position of other species across the disturbance gradient, particularly potential intermediate predators, we took extensive kicknet samples in each river and swept

nets through riparian vegetation to capture any terrestrial species that occurred in large enough numbers for analysis (~ 1 mg DW). We also searched for and handpicked common terrestrial invertebrates that had been found in previous surveys of these rivers (Chapter 2).

All samples were frozen at -20 °C prior to processing when they were sorted into genera, and at least 5 individuals per taxonomic group for large bodied invertebrates, and up to 30 individuals for smaller taxa were oven dried at 60 °C for 48 hours. For each taxonomic group the number and length of individuals analysed was the same across all rivers. Larger aquatic insects, i.e. those close to emerging as adults, were preferentially included in samples to ensure that isotope signatures were representative of the stages (subimagoes, adults, final instar larvae) most likely to be eaten by *D. aquaticus* (Williams 1979). The number of *D. aquaticus* collected from each river for individual analysis ranged from four to nine and we calculated the condition of these spiders using $(width_{abdomen} - width_{cephalothorax}) / width_{cephalothorax,}$ where a more negative number indicates better condition. Spider size was measured from two photographs of each spider on a 2 mm grid using the measure tool in Photoshop 7.

The digestive tract was removed from taxa that were not liquid feeders to ensure that isotopic measurements reflected assimilated body tissue only. Dried samples were ground to a fine powder and sent to the Waikato Stable Isotope Unit for analysis using a Europa Scientific 20/20 isotope analyzer. Isotope ratios are expressed in the δ notation according to $\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000$, where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standards were Pee Dee belemnite for carbon and atmospheric nitrogen for nitrogen and the precision of measurement was ± 1%.

Trophic positions of *D. aquaticus* and web spiders (*Haplinis* sp (Blest), Linyphiidae) were calculated from a two source mixing model (Post 2002b) using the mayfly *Deleatidium* and crickets as the basal $\delta^{15}N$ sources, while the trophic position of aquatic predatory caddisflies (Hydrobiosidae) and large predatory Megaloptera were calculated using *Deleatidium* alone as the basal member, as they feed only on aquatic prey. To calculate trophic position using a two source model (Post 2002b), the $\delta^{13}C$ values of the two sources were used to estimate the relative amount of nitrogen the focal consumer is likely to have obtained from each source. This necessitated that the $\delta^{13}C$ values of the focal consumer fell within the $\delta^{13}C$ values of the two sources.

Although this did not occur for some *D. aquaticus* individuals the $\delta^{15}N$ levels of both sources were very similar, (mean difference = 0.71 ‰ ± 0.16 across all rivers) and the proportion of $\delta^{15}N$ from each source would have had little impact on trophic position. Where the $\delta^{13}C$ value of *D. aquaticus* fell outside of the range in ^{13}C encompassed by crickets and *Deleatidium* we assumed that all the nitrogen was obtained from the source with the closest $\delta^{13}C$ value. Trophic enrichment of $\delta^{15}N$ was assumed to be 3.4‰ (Peterson and Fry 1987, Vander Zanden and Rasmussen 1999) although estimates range from 2 to 5‰ (Post 2002b). Since we were exploring relative relationships across the disturbance gradient the enrichment value used would not influence our conclusions. In addition, differences in fractionation between trophic levels across the disturbance gradient studied are unlikely to occur as New Zealand rivers contain a core of generalist insect taxa (Winterbourn 2000) and the taxa found at disturbed sites were generally a nested subset of those found at less flood-prone rivers.

Potential intermediate predators

We calculated the total number of predatory aquatic and terrestrial taxa for the eight rivers included in the stable isotope analysis from data collected in a large-scale survey in January 2005 (Chapter 2). Four Surber samples (0.09 m^2, 250 μm mesh) were taken from rivers and five terrestrial quadrats (0.25 m^2) were vacuumed alongside each river. Invertebrates were identified to genus, except for chironomids and terrestrial taxa, which were identified to family. Predatory aquatic taxa were identified from functional feeding group definitions in Winterbourn (2000).

Cannibalism mesocosms

To test the effects of non-guild prey availability and *D. aquaticus* density on cannibalism rates in conditions similar to those found at stable, intermediately disturbed and very disturbed rivers we carried out a mesocosm experiment. Spiders other than *D. aquaticus* were excluded to specifically investigate *D. aquaticus* cannibalism rates. We used spider density as a surrogate for habitat availability and crossed this with non-guild prey number. Sixteen paddling pools (1.5 x 1.2 x 0.4 m high, 1.8 m^2) were constructed with flowing water channels (0.15 m^2) set into the centre of each mesocosm. The surrounding area was covered in gravel and abundant rocks for spiders to hide under (Figure 4c). The pools were covered with netting to

prevent spiders escaping and to exclude predators like birds and cats. Two spider densities were chosen to mimic natural densities found at both stable and more disturbed rivers for the high density treatment, and at intermediately disturbed rivers for the low density treatments. Mesocosms were set up in randomized blocks in grassland near the University of Canterbury's field station at Cass, South Island, New Zealand, and supplied with water pumped from nearby Grasmere Stream. Mature female spiders were excluded from the experiment as they can be especially aggressive if mated (Kreiter and Wise 2001) and spiders were randomly assigned to mesocosms. Densities were five or two spiders per mesocosm for the high and low density treatments, respectively. Late instar *Nesameletus* mayfly larvae and tenebrionid beetle larvae were added to the mesocosms as aquatic and terrestrial food sources, respectively. Spiders were fed two beetles and 20 mayflies for the high food treatment and one beetle and five mayflies for the low food treatment every four days. Food levels mimic those found in stable rivers (high food) and very disturbed rivers (low food) based on dry weights (Chapter Two). Spiders were collected from the Kowai River on 11 November 2005, digitally photographed on a 2 mm grid, weighed and uniquely identified by a small dot of coloured acrylic paint on the cephalothorax. The experiment was run for 15 days and any spiders remaining at the end were identified, digitally photographed and weighed. Exuviae were also collected to aid identification of spiders that shed their identifying paint dot. Cannibalism was assumed if a spider was missing from a mesocosm and no body was discovered, although often *D. aquaticus* food pellets containing conspecific body parts were found. *D. aquaticus* could not escape from the mesocosms, which were searched thoroughly after the experiment and bodies were unlikely to decompose in 2 weeks.

Analyses

To investigate patterns in the spatial distribution of *D. aquaticus* across the disturbance gradient we used non linear regression between the river disturbance index scores and the standardized Morisita index of dispersion score (n=11). The same method was used to test patterns of trophic position (n=8) across the flood gradient.

The number of predatory taxa in both aquatic and terrestrial systems was tested against the river disturbance index using linear regression to investigate the

presence of additional predators, which could potentially form extra trophic levels increasing food chain length between the two base line $\delta^{15}N$ sources and *D. aquaticus.*

To test whether patterns in the trophic position of intermediate predators could bring about the quadratic pattern of trophic position of *D. aquaticus* observed across the disturbance gradient we fitted quadratic regressions to relationships of the trophic position of predatory hydrobiosid caddisflies and small linyphiid web spiders with the disturbance index. The trophic position of the predatory aquatic dobsonfly *Archichauliodes diversus* (Megaloptera) was also examined to determine if it occupied an intermediate trophic position between *D. aquaticus* and Hydrobiosidae. The density of other spiders across the disturbance gradient was also tested with regression to explore the availability of guild prey to *D. aquaticus.*

The proportion of spiders cannibalized and the proportion of survivors that increased in weight in the mesocosm experiment was tested with full factorial two-way ANOVAs using spider density and prey level as main effects with blocks. Post hoc Bonferroni tests were conducted to investigate differences between treatments.

All analyses were performed in Statistica (Statsoft ver 6) and variables were log (x+1) transformed where necessary to meet assumptions of heteroscedasticity and normality.

RESULTS

Dispersion

The standardized Morisita dispersion index was highest, indicating clumped population distributions, at both stable and more disturbed sites, whereas at sites more intermediate on the disturbance gradient the index score was close to 0, indicating randomly distributed populations (Fig 2a).

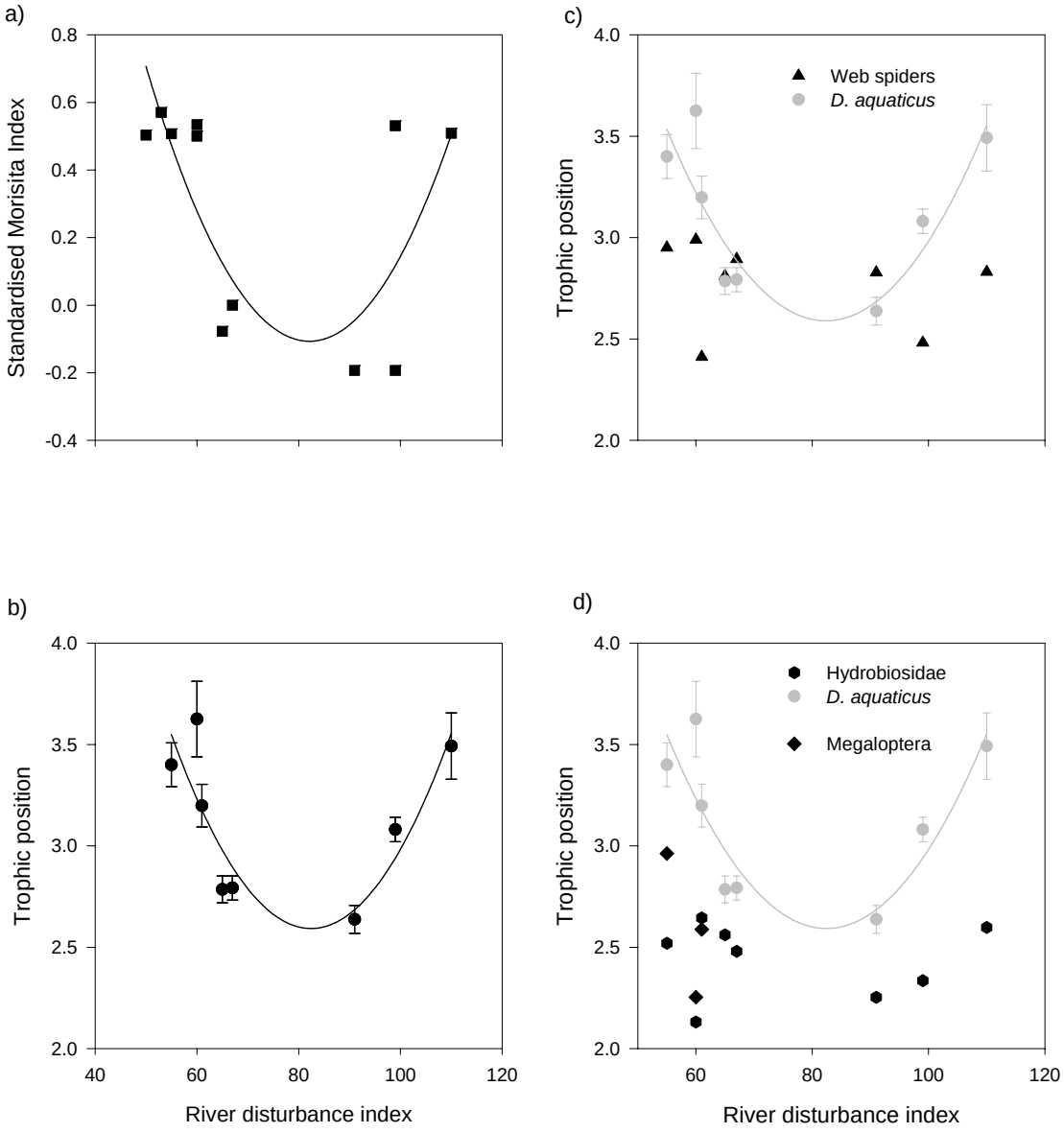

Figure 2 Spatial clumping of *D. aquaticus* was highest at both extremes of the flood disturbance gradient as measured by the standardised Morisita index of dispersion (a) ($F_{1, 8}$ = 7.58, P = 0.025, r^2 = 0.54, y = 5.21 + -0.13x + 0.0008x^2). The mean (± SE) trophic position of *D. aquaticus* indicated by δ^{15}N values ($F_{1, 5}$ = 13.42, P = 0.015, r^2 = 0.73, y = 11.15 + -0.21x + 0.0013x^2) was also highest at both extremes of the disturbance gradient (b) while the trophic position of web spiders (Linyphiidae) (triangles) (c), predatory caddisflies (Hydrobiosidae) (hexagons) and Megaloptera (diamonds) (d) showed no pattern across the flood gradient. Grey circles show the mean (± SE) *D. aquaticus* trophic position in (c) and (d).

Stable isotope analysis

The chosen baseline aquatic and terrestrial insects, mayflies and crickets, overlapped in their $\delta^{13}C$ at many rivers, thus they could not be used to separate the proportion of aquatic and terrestrial biomass assimilated by *D. aquaticus* across the flood gradient. However, the average trophic position of *D. aquaticus*, as indicated by baseline-corrected $\delta^{15}N$ values, was highest at the most stable and most disturbed rivers across the disturbance gradient and almost one trophic position lower at intermediately disturbed rivers (Fig 2b). The trophic position of free living predatory caddisflies (Hydrobiosidae) ($F_{2, 7} = 0.81$, $P = 0.50$) and web spiders (Linyphiidae) ($F_{2, 7} = 0.19$, $P = 0.83$) did not vary across the disturbance gradient and could not explain the pattern seen in trophic position of *D. aquaticus* (Fig 2c and d). The trophic position of the megalopteran A*rchichauliodes* was intermediate between those of predatory caddisflies (Hydrobiosidae) and *D. aquaticus* at only one of the three stable sites where they were found, indicating that they are unlikely to act as intermediate predators between these two taxa (Fig 2d). Starvation levels could not explain the differences in $\delta^{15}N$ values across the disturbance gradient (e.g. Adams and Sterner 2000, Oelbermann and Scheu 2002). Although spiders at more stable rivers had higher per capita non-guild prey availability, condition levels were similar (mean ± 1 SE, -0.12 ± 0.03, n=20) to those at more disturbed rivers (mean ± 1 SE, -0.07 ± 0.03, n = 21).

Potential intermediate predators

The total number of taxa and number of predatory taxa were generally higher at more stable rivers for both aquatic and terrestrial taxa (Fig 3a and b). The abundance of spiders other than *D. aquaticus* was higher at more stable rivers and declined linearly as river disturbance increased (Fig 3c).

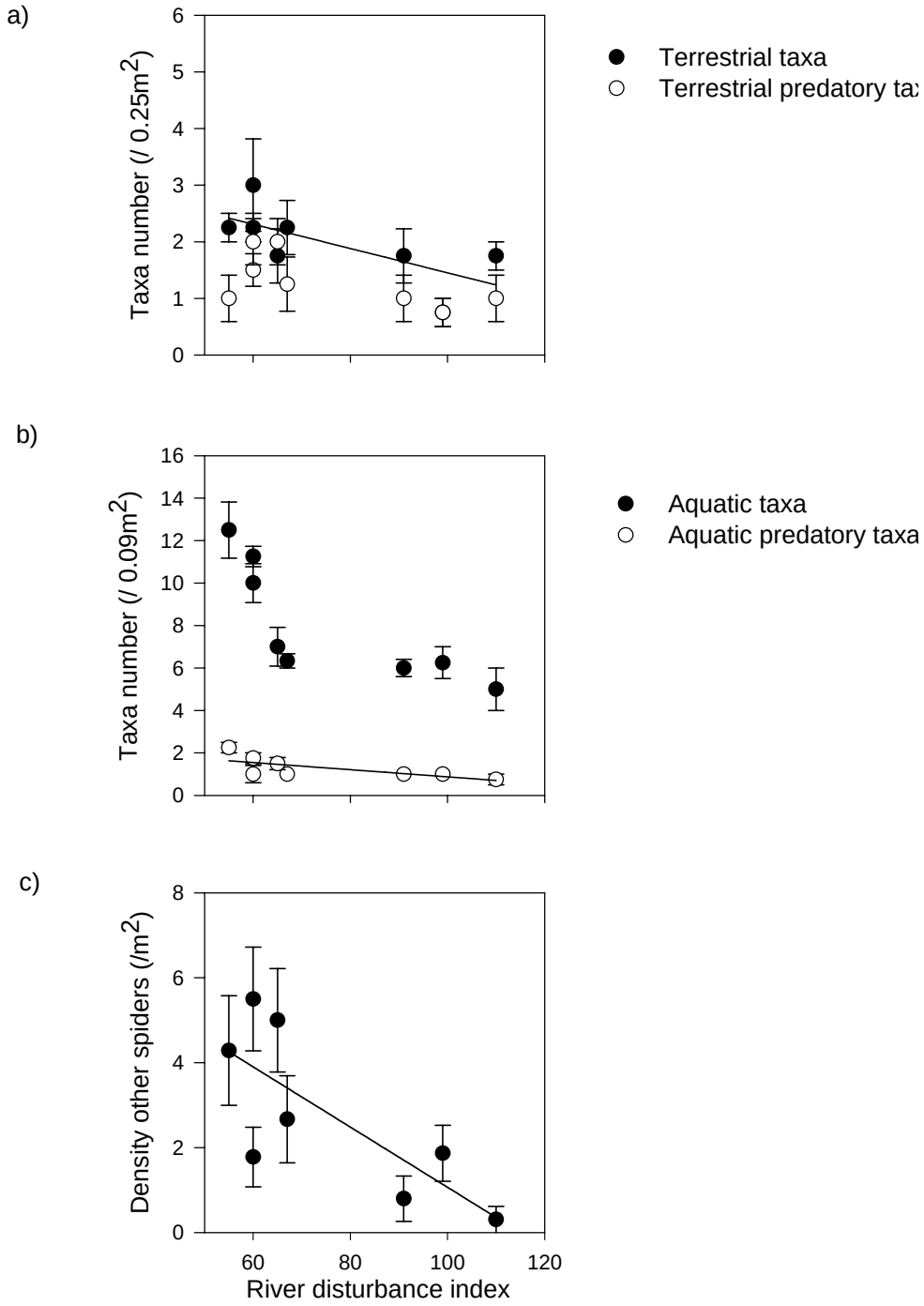

Figure 3 The number of terrestrial taxa (filled circles) and predatory terrestrial taxa ($F_{1, 6}$ = 5.58 , P = 0.06, r^2 = 0.48, y= 3.6 – 0.02x) (open circles) (a), the total number of aquatic taxa (filled circles) and predatory aquatic taxa ($F_{1, 6}$ = 5.73, P = 0.05, r^2 = 0.49, y = 2.57 – 0.01x) (open circles) (b) and the mean (± SE) density of spiders other than *D. aquaticus* (a) ($F_{1, 7}$ =8.2, P = 0.029, r^2 = 0.58) (c) all decreased across the disturbance gradient. Flood-prone rivers have a higher river disturbance index score.

Cannibalism mesocosms

There were significant density ($F_{1, 9} = 8.60$, $P = 0.17$) and food by density interaction ($F_{1, 9} = 9.16$, $P = 0.014$) effects on the proportion of spiders cannibalized in the mesocosms (Fig 4a). A post hoc Bonferroni test indicated that cannibalism in the low spider-low food treatment (intermediately disturbed river) was significantly lower than cannibalism in both the high spider-high food (stable river) and high spider-low food treatments (disturbed river). Cannibalism in the low spider-high food treatment was not significantly different from that in any other treatments. The proportion of surviving spiders that increased in weight was significantly affected by food availability ($F_{1, 9} = 11.71$, $P = 0.008$) and marginally by a food by density interaction ($F_{1, 9} = 3.84$, $P = 0.08$) (Fig 4b). In the high spider-low food treatment (disturbed river) significantly fewer of the spiders remaining increased in weight than in the high spider-high food treatment (stable river). The low spider-low food (intermediately disturbed river) and low spider-high food treatments were not significantly different from either of the other two treatments (Bonferroni post hoc test).

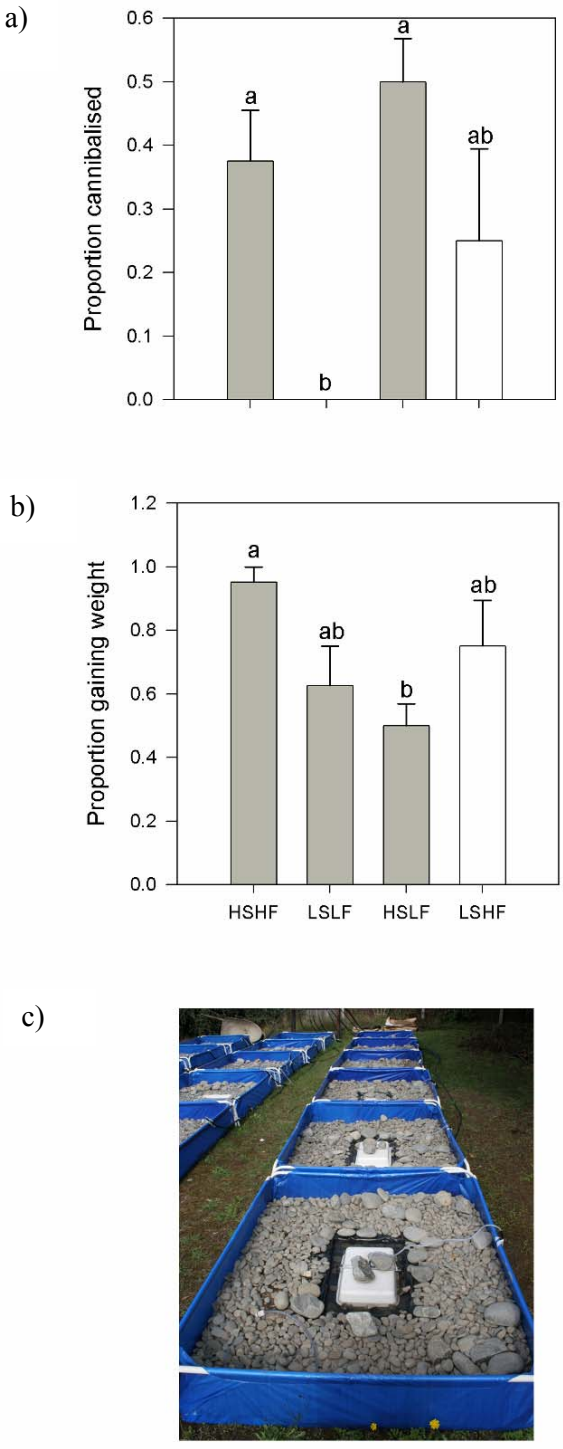

Figure 4 The mean (± SE) proportion of *D. aquaticus* cannibalized (a) and the mean (± SE) proportion of surviving spiders gaining weight (b) in a mesocosm experiment (c) in which food level (high and low food levels HF and LF, respectively) spider density (high and low spider density HS and LS, respectively) were manipulated. Letters denote significant differences indicated by Bonferroni post-hoc tests.

DISCUSSION

The cross-ecosystem transfer of resources can cause dramatic population and community level changes in the recipient system via increasing intraguild predation. However, the magnitude of these subsidies alone does not determine intraguild predation rates of consumers. Our results demonstrated that the influence of cross-ecosystem energy flows on strong biotic interactions in the recipient system was modified by habitat availability; the interaction of the two resources altered the abundance and spatial distribution of the consumers, determining rates of intraguild predation. Across the flood disturbance gradient the biomass of winged aquatic prey declined markedly with increasing flood disturbance, however the availability of suitable habitat for *D. aquaticus* was higher at food-prone rivers (Chapter 2). At the rivers where this mis-match in resources was greatest, spider populations were spatially clumped (4 m^2 scale). High density clumps of spiders occurred at infrequently flooded rivers, which had high levels of non-guild (aquatic insect) prey available, but were limited by habitat area (see Chapter 2). *D. aquaticus* populations were also clumped at flood-prone rivers where there were large areas of habitat but lower aquatic insect abundance than in more stable rivers. Clumping was brought about by spiders aggregating around stable vegetated islands close to the waters edge, which as well as being important nesting sites, may provide refugia during floods (pers obs. M. Greenwood). *D. aquaticus* populations at intermediately disturbed rivers were randomly distributed leading to lower small-scale densities.

Intraguild predation rates are usually density dependent (e.g. Buddle et al. 2003, Eitam et al. 2005) so we predicted that cannibalism rates among *D. aquaticus* would be highest at both extremes of the flood disturbance gradient. This prediction was supported by measurements of trophic position estimated from stable nitrogen isotope analyses. Trophic position of *D. aquaticus* across the flood disturbance gradient matched the u-shaped pattern of spider aggregation. Spiders at more stable and disturbed ends of the gradient had $\delta^{15}N$ values nearly one entire trophic level higher than those at the more intermediately disturbed sites. The length of the food chain below a focal predator can substantially affect its trophic position (Vander Zanden et al. 1999, Post 2002a), however, the trophic position of two intermediate aquatic and terrestrial predatory invertebrates (Hydrobiosidae and Linyphiidae), did not explain the variations in *D. aquaticus* trophic position. Similarly, the additional

large predatory insect found in stable rivers (*Archichauliodes diversus*) had a $\delta^{15}N$ signature similar to those of predatory caddisflies (Hydrobiosidae) and was intermediate between them and *D. aquaticus* only at the most stable river. Thus, its presence in the food web did not generally lead to the increase in observed trophic position of *D. aquaticus* at stable sites.

Differences in food chain length across the flood gradient are unlikely to explain the u-shaped trophic pattern exhibited by *D. aquaticus*. For example, Townsend et al. (1998) found the total number of species (algae, invertebrates and fish) in New Zealand stream food web declined as the intensity of disturbance increased, but mean food chain length showed no relationship with disturbance. Furthermore, theory suggests that intraguild predation should act to make the longest food chains occur at intermediate levels of productivity. In highly productive areas top predators can reach high densities and eliminate or nearly eliminate intermediate predators, thereby shortening realized food chain length (Holt and Polis 1997). Thus, differences in the number of feeding links below *D. aquaticus* could not explain the pattern in trophic position we observed.

Variation in intraguild predation rates, including cannibalism, is therefore the most likely explanation of the differences seen in the trophic position of *D. aquaticus* in rivers varying in flood disturbance. The effects of cannibalism on trophic position of the spiders cannot be separated from the more general case of intraguild predation based on the stable isotope results alone. Thus, other spider taxa, which were most abundant at the stable rivers could have formed a component of *D. aquaticus* diet at these sites.

Density dependent intraguild predation, particularly cannibalism is common but often linked to other factors, especially the availability of alternative prey (Fox 1975, Elgar and Crespi 1992, e.g. Wagner and Wise 1996, Rickers and Scheu 2005). To separate the mechanisms driving the field patterns in intraguild predation rates and to assay cannibalism rates in conditions similar to those found in natural rivers we designed a cannibalism mesocosm experiment. Cannibalism rates were highest in conditions simulating both stable (high food level-high spider density) and very disturbed rivers (low food-high density) and no cannibalism was found in conditions matching those of intermediately disturbed rivers (low food-low density). This evidence supports the results of the stable nitrogen analyses that *D. aquaticus* occupies a higher trophic position at either end of the disturbance gradient, and that

this difference is likely to be caused by differences in intraguild predation and cannibalism rates. At disturbed rivers high cannibalism rates were likely to have been brought about by limitations in the availability of other prey organisms (e.g. Leonardsson 1991). However, at the more stable rivers where food availability was greater, the limitation in usable habitat for spiders led to high densities which would have increased encounter rates between individuals (e.g. Moksnes 2004). Rates of cannibalism cannot be extrapolated directly from our mesocosm experiment to field conditions, particularly due to the short time-frame of the experiment and the prevention of migration. However, the relative rates of cannibalism across the treatments combined with the stable isotope results, and field patterns in the spatial distribution of *D. aquaticus* strongly suggest that relative rates of intraguild predation, especially cannibalism, are markedly higher in more stable and disturbed river populations than those that occur at rivers more intermediate on this disturbance gradient.

The variations in cannibalism rates in the mesocosms were driven by the differences in density. However rates of cannibalism were higher in the low density treatments when more non-guild prey were available. Although this situation (high food, low spider density) did not occur in the field, it does imply that the presence of higher prey levels may have stimulated the spiders into more active searching and perhaps increased conspecific encounter rates.

Effects of food availability were also reflected in the proportion of surviving spiders that increased in weight over the course of the experiment. More spiders increased in weight in the high food treatments than when food availability was lower. Therefore, although cannibalism rates were similar under very stable and very disturbed conditions, longer term effects of food availability may affect populations differently and need further investigation. For example, as small-scale spider densities were similar at very stable and more disturbed rivers, individuals at the more stable sites should have higher per capita prey availability. This could lead to changes in the size distribution of the populations, female fecundity (Kreiter and Wise 2001), or between-patch migration rates, all of which could impact cannibalism rates. Immigration and emigration rates can act to increase or negate rates of density dependent cannibalism, respectively, and recruitment into patches must occur in the field to maintain the high densities of spiders found at stable and very disturbed rivers if cannibalism occurs frequently. Migration rates between patches must be relatively

similar across the environmental gradient for cannibalism rates to be able to be predicted by the densities observed at each site. In addition, cannibalism itself can influence spatial distribution with size classes segregating themselves spatially (e.g. Leonardsson 1991, Jormalainen and Shuster 1997) or individuals becoming evenly spaced (Polis 1981).

Our results also indicate that the influence of transfers of resources across ecosystem boundaries will vary with spatial scale. Although we found a u-shaped relationship between *D. aquaticus* density and disturbance at a 4 m^2 scale, we found that at a 100 m reach-scale, populations were largest at intermediately disturbed rivers (Chapter 2). *D. aquaticus* populations at stable and disturbed rivers at the 100 m reach-scale were small because they were limited by resources. In stable and disturbed rivers cannibalism rates were strong in isolated patches, yet along the majority of the riverbank there were relatively few individuals. At intermediately disturbed rivers cannibalism rates were low but spiders were likely to be distributed more uniformly. The consequences of this for population and community structure need to be investigated further.

Our research shows that cross-ecosystem transfers of energy can not only have large impacts on rates of intraguild predation, a strong biotic interaction that is capable of structuring recipient communities through top-down effects, but also that such impacts are mediated by interactions between the magnitude of the subsidy and in-situ resource availability for the consumer. These finding have broad implications for studies concerned with understanding and ultimately predicting outcomes of biotic interactions between adjacent ecosystems.

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Chapter 4

Flood disturbance-related influences on the size structure and condition of a riparian predator

ABSTRACT

Cross-ecosystem transfers of resources have the potential to have large impacts on the life history traits of consumers in adjacent systems by changing the nature and availability of prey. However, large-scale influences, such as disturbance, that control the magnitude of prey subsidies are likely to modify these effects. Here I used a flood disturbance gradient, across which the abundance of aquatic insect taxa varied, to investigate impacts of cross-ecosystem subsidies on the life history traits of a riparian fishing spider, *Dolomedes aquaticus*. These spiders rely on adult aquatic insects for a large proportion of their diet. In laboratory experiments, increased prey availability hastened the first moult of the spiders after winter and decreased the propensity for cannibalistic interactions of individuals of the same size. However, despite these positive influences of increased food supply, the highest abundance and proportion of large females of egg-sac bearing size were not at the least flood-prone rivers, where aquatic prey availability was highest. Instead other influences associated with the disturbance regime, such as habitat, which alters rates of cannibalistic interactions between *D. aquaticus* individuals, as well as the direct mortality effect of floods modified the influence of cross-ecosystem subsidies on the life history traits of these spiders.

INTRODUCTION

Investigating the influence of cross-ecosystem subsidies of prey on the life history traits of consumers is a crucial step towards understanding and predicting the complex effects that spatial subsidies can have on both recipient and donor ecosystems. Food resource availability often influences growth rates, survival or longevity of individuals, leading to changes in life history characteristics (Mayntz et al. 2003). Thus, cross–ecosystem prey transfers have the potential to have large impacts on the

expression of life history traits of predators in adjacent ecosystems (Sabo and Power 2002). The observed life history traits of organisms are a result of many complex interacting factors: the temperature and stability of the environment (Stearns 1992), resource availability (Kreiter and Wise 2001) and the timing of its availability (Phillips 2005), predation pressures, and the flexibility of life history traits in response to these factors (Abrams et al. 1996). Prey availability often brings about changes in the density and or abundance of predators, and increases in the amount of food available can have positive impacts on many life history traits (Mayntz et al. 2003). For example, an increase in prey abundance can result in alterations in the timing and/or size at maturation, and hence reproductive success of the consumer. However, trade-offs with other factors, such as mortality risk, can also limit when an increase in food will lead to such positive effects (Abrams 1991, Stearns 1992). Subsidies of prey from adjacent ecosystems can influence the abundance and growth rates of recipient consumers (Sabo and Power 2002, Stapp and Polis 2003, Paetzold et al. 2006), but the influence of such allochthonous resources on the life history and size structure of recipient consumer populations is poorly understood.

The ability of consumers to benefit from and alter their life histories in response to prey subsidies may also be affected by the nature of the ecosystem boundary. Changes to the structural nature of the boundary, often caused by large-scale factors such as physical disturbances, alter the magnitude and direction of energy flows between adjacent ecosystems (Chapter 2). Such changes to ecotones may also alter the suitability of habitat for potential consumers of the resource subsidy and hence the ability of the consumer to respond functionally and numerically (Chapter 2). In addition, disturbances themselves, particularly their timing and predictability, can have marked impacts on the evolution and flexibility of life history traits of species (Robinson et al. 1992, Lytle 2002). For example, the unpredictable flood regime of New Zealand rivers has been linked to aseasonal and flexible life history traits in aquatic insects (Winterbourn et al. 1981, Scarsbrook 2000), characteristics which may also apply to riparian consumers of cross ecosystem subsidies that inhabit the floodplain.

River flood regimes create a gradient of disturbance impacts on aquatic and riparian conditions by dramatically altering the physical nature of the aquatic-riparian boundary. Floods change the suitability of the riparian zone as habitat for terrestrial consumers (Bonn et al. 2002, Ballinger et al. 2005) as well as the abundance of

aquatic insects available as allochthonous prey (Chapter 2). Since many riparian consumers depend on emerging aquatic insects as prey (Sanzone et al. 2003) floods can be expected to have large impacts on predator life history traits through changes to habitat and prey resource availability, as well as via direct flood-related mortality effects.

In Chapters 2 and 3 I demonstrated that changes to allochthonous prey and habitat availability brought about by differences in flood disturbance in inland Canterbury rivers affect the population size, small-scale density and relative frequency of intraguild predatory interactions of a riparian fishing spider *Dolomedes aquaticus*. Spatial subsidies from benthic aquatic insects with a winged adult phase were much higher at stable rivers than at those more often disturbed by floods (Table 1). However, the availability of usable spider habitat (loose, unembedded river bank rocks) was much lower at the least flood-prone sites (Table 1). At more disturbed rivers, aquatic prey levels were low, but large areas of habitat were available to the spiders. The combination of these factors led to aggregated spider populations at small scales alongside stable and very disturbed rivers, whereas populations at intermediately disturbed rivers were more evenly distributed (Table 1). In turn, cannibalism rates were highest at both ends of the disturbance gradient, most likely because of the high small-scale densities of spiders at these rivers. Cannibalism is common in *Dolomedes* spp. (Zimmermann and Spence 1989, Johnson 2005) and has been hypothesized to influence phenology, microhabitat use and population dynamics of the spiders (Zimmermann and Spence 1989). Food availability also often influences cannibalism rates (Fox 1975), which in turn can have large impacts on life histories (Elgar and Crespi 1992). Thus, in a species like *D. aquaticus* with a propensity for cannibalism, low food availability and starvation are likely to lead to changes in the size structure of populations and the life history traits of individuals (Figure 1).

In this study I investigated how flood disturbance regime influenced the expression of life history traits of *D. aquaticus*. Particularly their population size structure and condition. I hypothesised that the unpredictable nature of New Zealand's flood prone rivers would lead to more asynchronous development of populations than in North American *Dolomedes* species. In addition I investigated how the nature of the riparian boundary along a flood disturbance gradient affected the influence of allochthonous resource levels on the size class structure and condition factor of the

spiders. I predicted that increased allochthonous prey availability and lower flooding at stable rivers would have positive impacts on the growth rates, size and hence reproductive success of *D. aquaticus* individuals. These factors, combined with high rates of cannibalism at less flood-prone rivers, in which large body size is usually an advantage, led me to hypothesize that a higher abundance of large spiders, particularly females, would occur at less flood prone rivers. However, other disturbance-mediated factors, such as habitat availability, may alter the ability of the spiders to benefit from cross-ecosystem subsidies across a flood gradient. In addition, the variation in cannibalism rates across the disturbance gradient is likely to alter population size structure. I used field surveys to obtain life history information on *D. aquaticus* across the disturbance gradient and experiments to determine the influence of prey availability on growth and cannibalism rates.

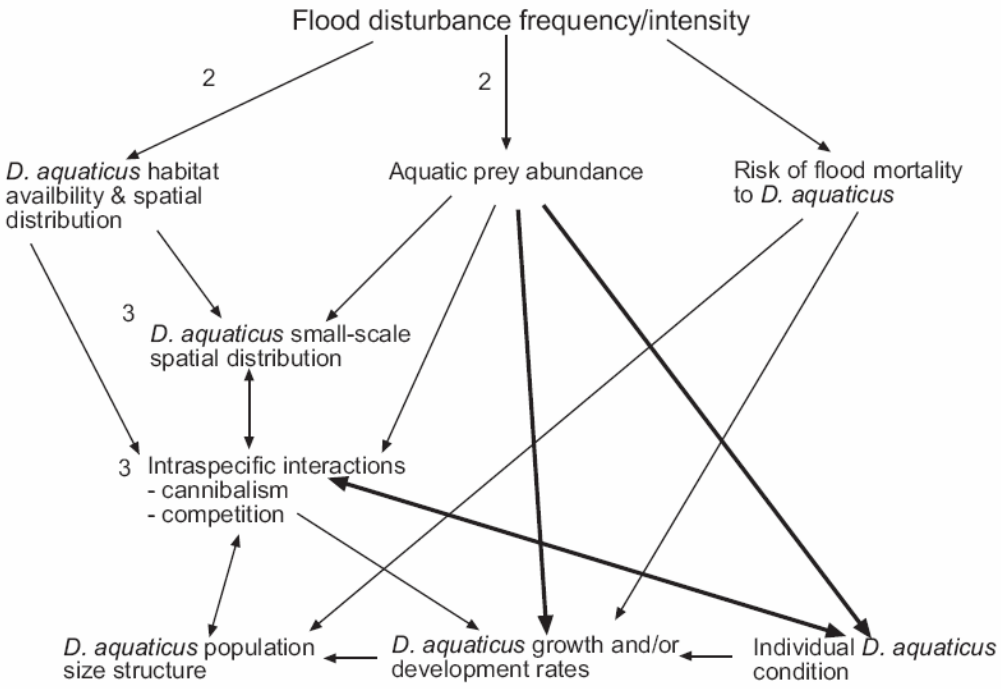

Figure 1 Diagram of potential effects of flood regime on the life history traits of *D. aquaticus.* Numbers indicate the chapters containing supporting data for the linkages. Bold arrows indicate linkages investigated in this chapter. Other potential contributing factors are examined in the discussion.

Table 1 Patterns of aquatic prey and habitat availability, density and cannibalism of *Dolomedes aquaticus* across a flood disturbance gradient in the Waimakariri catchment, South Island, New Zealand. For river identities see Appendix I.

	Flood regime		
	Stable	Intermediate	Disturbed
Aquatic prey abundance*	Highest	Low	Lowest
Useable habitat*	Low	Higher	Highest
Reach-scale density (600 m^2 bank area)*	Low	High	Low
Patch-scale density (4 m^2 area) †	High	Low	High
Cannibalism rates†	High	Low	High

* Chapter 2
† Chapter 3

METHODS

Field patterns

Data used to discern life history patterns were obtained from spider surveys undertaken at 12 rivers in the Waimakariri River catchment between May 2004 and April 2006. These rivers ranged across a flood-disturbance gradient from stable spring-fed systems to a large, frequently disturbed, braided river (Appendix I). Flood disturbance was measured using the visually estimated river disturbance (channel stability) index (Pfankuch 1975) and painted tracer rock particles. Details of the how the methods were conducted are included in Chapter 2. A high degree of correlation was found between the two methods ($r^2 = 0.85$) and for this chapter only the river disturbance index is used. This index ranges from 32 to 152, a higher score indicating a less stable (more disturbed) river. The riverbanks of all study rivers were largely unvegetated and were dominated by bare cobbles or boulders. Rivers were surrounded by tussock grassland with occasional shrubs.

Initial spider surveys were conducted up to five metres from the river edge, however from October 2005 – April 2006 the distance was reduced to three metres when it became apparent that almost all spiders lived within three metres of the river bank. Banks were searched by overturning stones while moving systematically along the riverbank. Each spider was digitally photographed twice on a 2 mm grid at a constant distance from the camera and cephalothorax and abdomen width were measured with the measure tool in Photoshop 7. Spider size was calculated relative to the 2 mm grid and recorded as the average from the two photographs. A condition index (C.I.) modified from De Vito et al. (2004) was developed as:

$$\text{C.I.} = \frac{\left(\textit{abdomen width} - \textit{cephalothorax width}\right)}{\textit{cephalothorax width}} \qquad \text{Eq 1.}$$

The ratio of abdomen width to cephalothorax width has been often used previously to quantify the current condition of a spider (e.g. DeVito et al. 2004) as cephalothorax width is fixed between moults yet abdomen width varies depending on the feeding history of the individual. A positive index indicated that the spider's abdomen was wider than its cephalothorax and the individual was defined as being in 'good' condition. Spiders with an abdomen narrower than their cephalothorax were defined as in 'poor' condition. Mature male spiders were recognized by their bulbous palps and reddish colouration, but mature female spiders were more difficult to distinguish from non-sexually mature juveniles. The epigynum on the underside of the abdomen becomes sclerotised when the spiders are sexually mature. However, this sclerotisation was difficult to detect even under a microscope due to prolific hairs surrounding the epigynum. As it was not feasible to examine the epigynum of live spiders in the field large juvenile spiders and sexually mature females were not distinguished. However, 85% of spiders that were found with eggsacs had a cephalothorax width greater than 9 mm (n=29), thus non-male spiders over this size were almost certainly sexually mature females. As male spiders mature generally at a cephalothorax width of 5 – 7 mm, all spiders > 9 mm were classified as 'female'. The cephalothorax and eggsac width of females (where applicable) were measured, as eggsac size can be related to fecundity (Kreiter and Wise 2001).

To measure variation in size structure and condition of populations across the disturbance gradient I calculated the coefficients of variation of cephalothorax width and the condition index, respectively, of all individuals collected at each river in each

season. To remove negative numbers from the coefficient of variation of condition a constant of 1 was added to all values before calculation.

Food level experiment

To investigate the influence of food abundance on spider growth rates I housed *D. aquaticus* individuals in the laboratory and controlled prey levels. I collected a total of 36 *D. aquaticus* of random size and gender from three of the survey rivers (Appendix I). Spiders were housed individually in round transparent plastic containers (32 cm diameter, 15 cm high) with 4-5 cobbles for habitat and a small pool of water. Containers were covered with mesh to prevent spiders and prey animals escaping and kept in a shed on the University of Canterbury grounds with outside ambient temperature and an artificial light period of 10:14 (L : D).

Spiders were collected on 1 June 2004, digitally photographed, weighed and randomly assigned to one of the two food treatment levels (n=18 per treatment). They were fed housefly and beetle larvae every three days for the first three weeks, the numbers of prey items being adjusted so that approximately 100 % (low food treatment) and 60 % (high food) of the food added was eaten. This equated to five and one houseflies in the high and low treatments, respectively. Feeding frequency decreased throughout winter as the spiders became less active, and was adjusted so the same proportion of prey were being eaten. Tenebrionid beetle larvae were substituted for houseflies on three occasions and fed at the same rates. All spiders were re-photographed and weighed after three months (31 August) and the experiment was then left to run for another two months to collect information on timing of the first moult after winter. Spiders were fed in the same manner as above for the rest of the experiment.

Spider cannibalism experiment

One of the ways prey availability could affect *D. aquaticus* life history strategies is by changing the propensity for cannibalism to occur, as such intraspecific predatory interactions can have a large impact on population size structure and stability. Food availability alters the condition of spiders, thus to assay the influence of spider condition on propensity for cannibalism we paired spiders of similar sizes but different condition and measured time taken for cannibalism to occur. Three treatments: ‘poor’ – ‘poor’ condition, ‘poor’ – ‘good’ condition and ‘good’ – ‘good’ condition pairs were set up with five replicate pairs of each. Spider pairs were

collected from the same three rivers as for the growth experiment and were of similar size (mean ± SE = 0.18 ± 0.04 g weight) and the same sex, within a pair. Two of the pairs were male and the rest were either juveniles or females. Individuals were photographed, weighed and marked with an identifying paint dot before being added to containers similar to those used in the food level experiment. The experiment began on 9 September 2004 and was checked every 2-3 days for cannibalism for 6 weeks. Spiders were fed two houseflies per container every 3-4 days (a low food level). As spiders are unlikely to eat dead prey, cannibalism was assumed to have occurred when a complete or partial food pellet containing conspecific body parts was found.

Analyses

I investigated patterns in seasonal size distribution of field populations by combining data from all rivers. To explore specific differences associated with the flood regime rivers were used as replicates in regression analyses (n = 12). As *D. aquaticus* is relatively inactive during autumn and winter months, and most of the growth and reproductive output occurs during the warmer months, only data collected in spring and summer were used for these analyses. They included counts of the total number of spiders collected at each river in spring and summer and the proportion of these spiders that were small spiders, 'females', males and individuals of 'good' condition across the disturbance gradient. Small individuals were defined as those < 5 mm cephalothorax width as 99.98 % of males matured at a larger size than this (females mature at ~ 8-9 mm cephalothorax width) (n= 283). As female condition can affect reproductive success and is largely influenced by both juvenile and adult feeding patterns (Kreiter and Wise 2001) I also investigated patterns in condition of juvenile and female spiders across the disturbance gradient. Potentially ovigerous 'females' with a condition index > 0.1, indicating a swollen abdomen (see Zimmermann and Spence 1992) were excluded as their highly positive condition was not comparable to that of other individuals.

Spider weight and spider condition after two months in high and low food treatments, the effect of spider condition on the timing of the first moult after winter and the time taken to cannibalise a spider of the same size were analysed using linear regressions with spiders as replicates.

All analyses were performed in Statistica (version 6, Statsoft) and variables were log (x+1) transformed where necessary to meet assumptions of normality and

heteroscedasticity. Rivers were excluded as replicates if there were fewer than 10 individuals with the variable being investigated.

RESULTS

Field survey patterns

Population structure

Most size classes of *D. aquaticus* were present in all seasons at all sites. However, the distribution was skewed towards small individuals in spring (Fig 1a), with intermediate-sized individuals dominating in summer (Fig 1b). In autumn, a bimodal size distribution occurred with two broad size classes (year classes) predominant. A similar pattern of size structure was seen in all rivers across the disturbance gradient. Few very large and very small individuals were present in autumn and winter (Fig 1c and d), although some large females (i.e., > 9 mm cephalothorax width) appeared to have over-wintered. Females with eggsacs and nests containing live young were observed between December and April; males and females were found under the same rock in all seasons.

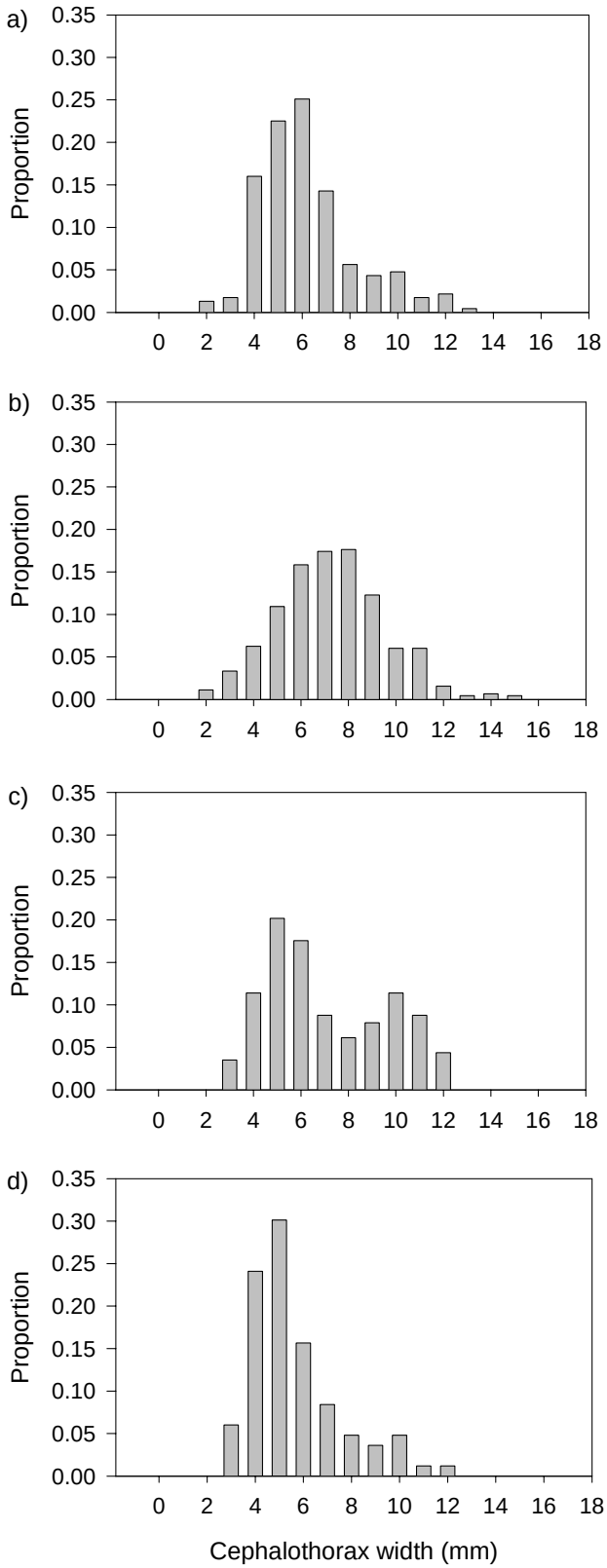

Figure 1 Frequency distributions of *D. aquaticus* cephalothorax width in (a) spring (n = 231), (b) summer (n= 448), (c) autumn (n = 114), and (d) winter (n = 83) across all study rivers.

Flood regime effects

No significant differences were found in the total number of spiders collected during summer at a site across the disturbance gradient (linear regression, $r^2 = 0.0005$, $F_{1, 9,} = 0.004$, $p = 0.94$, quadratic regression, $r^2 = 0.75$, $F_{1, 8} = 0.75$). However, the total number of small spiders (< 5 mm cephalothorax width) collected showed a peak-shaped unimodal pattern across the disturbance gradient (Fig 2a). In addition, the proportion of total spiders collected at each river that were small had a similar shaped relationship with the highest proportion of small spiders at intermediately disturbed rivers, where they accounted for up to 40 % of the population (Fig 2b). Both the total number of female spiders collected and proportion of total spiders collected that were female > 9 mm cephalothorax width increased with flood disturbance (Fig 2c & d). In contrast, the proportion of males showed a significant u-shaped unimodal relationship across the disturbance gradient (Fig 2f), although the number of males showed no significant pattern (Fig 2e). Thus, the relationship demonstrated by the proportion of males is likely to have been a consequence of the proportions of juveniles and females across the disturbance gradient. In any season other than summer there was no significant difference in the proportion of males and no difference in the average or maximum size of males across the disturbance gradient.

The coefficient of variation of cephalothorax width followed a peak-shaped unimodal pattern across the disturbance gradient with spiders of more variable width at intermediately disturbed rivers compared to more stable and disturbed rivers (Fig 3a). Spider condition also varied across the disturbance gradient; the proportion of spiders in 'good' condition (i.e., abdomen width ≥ cephalothorax width) being highest at stable rivers and lowest at rivers intermediate on the flood disturbance gradient during summer (Fig 3b). The coefficient of variation of condition of juvenile and mature females, with potentially ovigerous individuals excluded, was lowest at stable rivers and increased with river disturbance during summer (Fig 3c). Female cephalothorax width and eggsac diameter were positively correlated ($r^2 = 0.80$, $F_{1, 12} = 44.1$, $p<0.001$, eggsac diameter (mm) = -1.53 + 1.65 cephalothorax width (mm)).

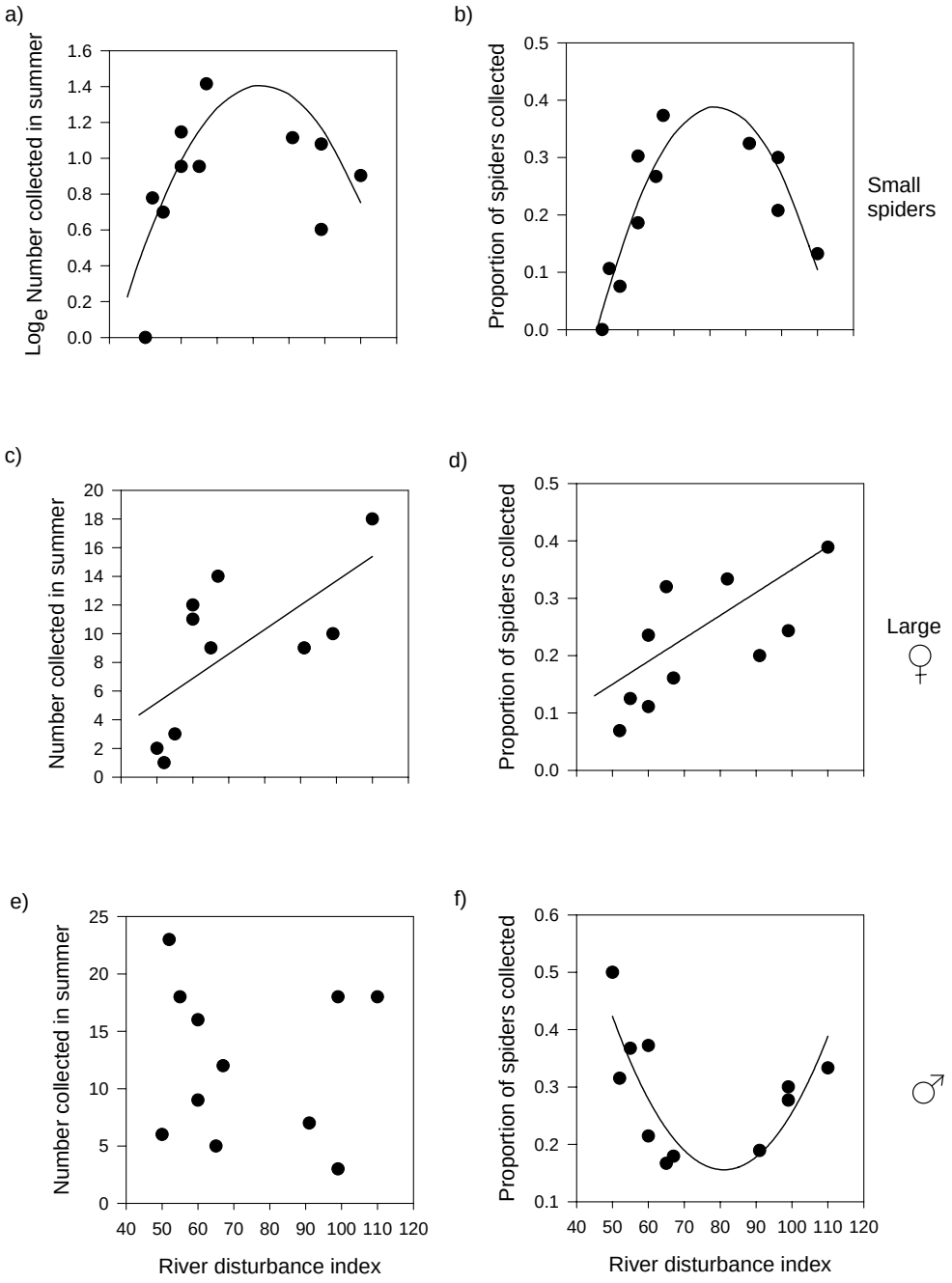

Figure 2 The numbers and proportions of small spiders, large females and males collected from all sampling occasions in summer in relation to habitat disturbance. Small spiders have a cephalothorax width < 5 mm whereas females have a cephalothorax width > 9 mm. A large river disturbance index (RDI) indicates a river more disturbed by floods. The relationships shown are described by (a) proportion small spiders $r^2 = 0.82$, $F_{1, 8} = 32.0$, $p = 0.0005$, proportion = -1.98 + 0.06*RDI – 0.0004*RDI^2), (b) total number small spiders collected ($r^2 = 0.48$, $F_{1, 8} = 6.39$, $p = 0.035$, Log_e(number) = -4.35 + 0.14*RDI – 0.00085*RDI^2), (c) proportion 'female' spiders > 9 mm cephalothorax width $r^2 = 0.48$, $F_{1, 8} = 7.34$, $p = 0.027$, proportion = - 0.05+ 0.004*RDI and (d) total number of them collected $r^2 = 0.48$, $F_{1, 8} = 6.49$, $p = 0.034$, number = -3.31 + 0.17*RDI and (e) the proportion $r^2 = 0.65$, $F_{1, 8} = 13.45$, $p = 0.006$, proportion = 1.98 – 0.045*RDI + 0.0003*RDI^2 and (f) total number $r^2 = 0.18$, $F_{1, 8} = 1.76$, $p = 0.22$ of male spiders collected.

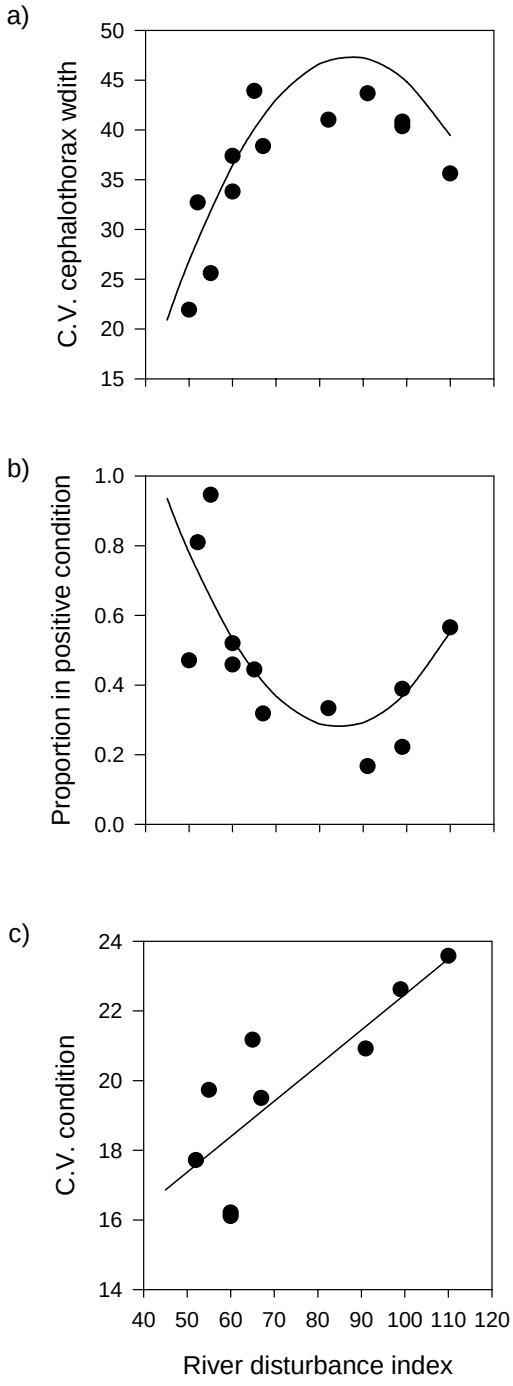

Figure 3 (a)The coefficient of variation of cephalothorax width during summer, (b) the proportion of spiders in "good" condition (i.e. abdomen width ≥ cephalothorax width) in spring and (c) the coefficient of variation of condition with male and potentially ovigerous female spiders (> 9 mm cephalothorax width, > 0.1 condition factor) excluded during summer across the flood disturbance gradient. A higher number on the river disturbance index (RDI) indicates a river more disturbed by floods. The relationships shown are described by (a) r^2 = 0.78, $F_{1, 9}$ = 17.58, p = 0.002, coefficient of variation of cephalothorax width = -66.15 + 2.61*RDI – 0.015*RDI^2, (b) r^2 = 0.59, $F_{1, 9}$ = 7.01, p = 0.027, proportion good condition = 3.28 – 0.071*RDI + 0.0004*RDI^2 and (c) r^2 = 0.66, $F_{1, 9}$ = 13.53, p = 0.008, coefficient of condition = 12.27 + 0.10*RDI.

Food level experiment

The condition of spiders at the end of the feeding experiment was related to their weight. As spider weight increased condition declined regardless of feeding regime (Fig 4a). Thus, even in the high food treatment larger spiders were not being feed enough to enable them to gain condition. However, the largest spiders did not follow this pattern. Instead they were in better condition than would have been predicted by their weight. Spider condition affected the timing of the first moult after winter. Spiders in poorer condition took up to six weeks longer to moult than those in good condition at the beginning of spring (Fig 4b). Source river had no effect on the results.

Spider cannibalism experiment

All spider pairs in the 'poor'-'poor' treatment engaged in cannibalism, as did three pairs in the 'good'-'poor' treatment and one pair in the 'good'-'good' treatment. In all cases the 'poorer' conditioned spider was the predator. In addition, the initial condition of similar sized spiders introduced to each other affected the time taken for the spiders to cannibalise. Spiders that were in worse condition cannibalized similar sized spiders sooner (Fig 4c). All spiders were within 0.04 g weight of each other and size difference was not significantly related to time taken to cannibalise ($r^2 = 0.33$, $F_{1, 8} = 3.46$, $p = 0.11$). Adult males of other *Dolomedes* species rarely feed (Kreiter and Wise 1996) or cannibalise conspecifics (Zimmermann and Spence 1989), however one male-male pair in the cannibalism experiment did engage in cannibalism.

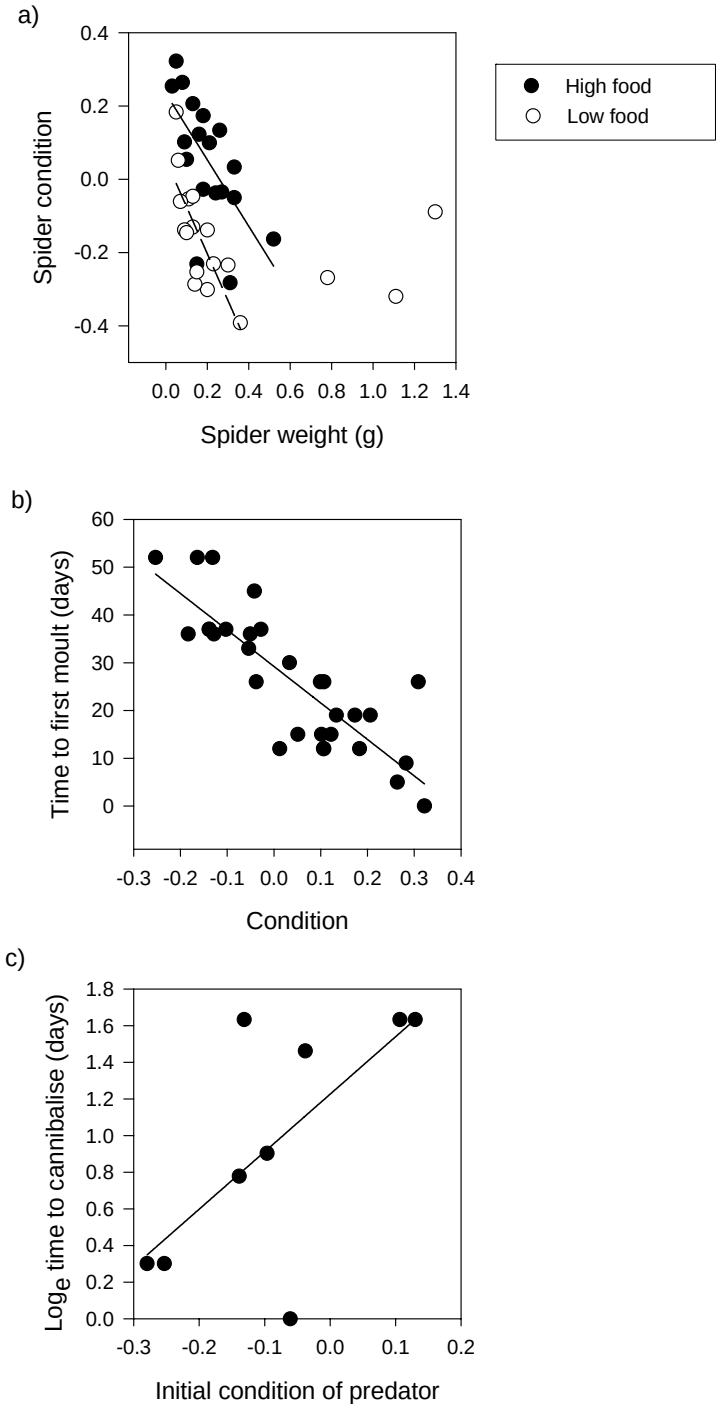

Figure 4 (a) The effect of high and low food treatments on the condition of *D. aquaticus* of a range of body sizes, (b)the influence of spider condition on the timing of the first moult after winter, and (c) length of time taken to cannibalise an individuals of the same size. The statistics for the relationships shown are (a) High food; $r^2 = 0.43$, $F_{1, 17} = 12.23$, $p < 0.01$, equation: spider condition = 0.23-0.91*weight, Low food; $r^2 = 0.59$, $F_{1, 14} = 19.16$, $p < 0.001$, equation: spider condition = 0.05-1.28*weight. The first moult of the growth experiment (b) occurred on 15 September and the relationship was significant with $r^2 = 0.74$, $F_{1, 29} = 66.68$, $p < 0.0001$, the equation is: time to first moult (days) = 29.21 - 76.4*Condition. The relationship between spider condition and time to cannibalise c) is $\log_e$ (time to cannibalise) = 1.22 +3.14*condition, $r^2 = 0.45$, $F_{1, 8} = 5.71$, $p = 0.04$.

DISCUSSION

D. aquaticus life history and a comparison with North American species

Mature males and large 'females' of *D. aquaticus* were found in all seasons in the Waimakariri catchment and populations showed a relatively asynchronous life cycle, with most size classes present in all seasons and under all flood disturbance regimes. In contrast many North American *Dolomedes* species have more seasonal and synchronous life cycles. For example, *D. triton* overwinters as large juveniles and reaches sexual maturity in 2-3 moults after icemelt in Central Alberta, with males developing approximately one week before females (Zimmermann and Spence 1992). The extended period during which *D. aquaticus* nests occurred (December to April), and the ability of females to produce multiple eggsacs per year (M. Greenwood pers. obs., Carico 1973) made the identification of cohorts difficult. However, the most likely life cycle length was two years with some mature females having the potential to survive into a third summer. This is comparable to the situation found in most Nearctic *Dolomedes*, which reach sexual maturity in about two years (Carico 1973, Kreiter and Wise 1996).

Differences in life cycle seasonality between New Zealand and North American *Dolomedes* species may be related to the predictability of the river disturbance regime, which can have strong impacts on species life history traits (Robinson et al. 1992, Iwasa and Levin 1995, Lytle 2001). The unpredictable flood regimes of most New Zealand flood-prone rivers have been hypothesized to have had a significant impact on the life histories of aquatic insects (Winterbourn et al. 1981, Scarsbrook 2000), many of which are asynchronous, opportunistic and flexible (Scarsbrook 2000). The population dynamics and life history traits of riparian organisms that inhabit the floodplain are also likely to be influenced by the flood regime (Stelter et al. 1997, Framenau et al. 2002). *D. aquaticus* occurs close to river margins, (typically within 3 m) and in rivers with unconstrained channels, such as my study sites, floods which overtop the banks or cause channel movement could result in significant mortality of small individuals or nestlings. In addition, adults of insects with aquatic larvae are a major component of the diet of *D. aquaticus* (Williams 1979) and the long emergence and adult flight periods of many of New Zealand's aquatic insect fauna leads to their presence in many months (Winterbourn 1997). This situation is likely to dampen seasonal differences in aquatic prey availability that can

occur in systems with more synchronous aquatic insect emergence (e.g. Nakano and Murakami 2000), and combined with more mild winters than are found in many Nearctic regions, could lead to the spiders having more extended growth and reproductive periods.

Environmental stability mediates the magnitude of the aquatic subsidy and its effects on population size structure

In spring, up to 90 percent of spiders at stable rivers, where aquatic prey abundance was highest (Chapter 2), were in good condition but only half were in good condition at more flood-disturbed rivers. Positive impacts on growth rate, body size at maturation and hence fecundity could be expected in stable environments where food availability is high (Stearns 1992, De Block and Stoks 2004). Laboratory studies showed that spiders in good condition moulted significantly sooner after winter. Therefore, spiders at more stable rivers may grow or develop faster, potentially leading to increased size at maturation and increased reproductive success, as larger female *D. aquaticus* had larger eggsacs. However, the proportion (and actual number) of large 'female' spiders within the size range for producing an eggsac (> 9 mm cephalothorax width) was lowest at the most stable rivers and highest at the most flood-prone rivers where aquatic prey were more scarce (Chapter 2).

Although, flooding decreases food availability and increases mortality risk it also increases the availability of *D. aquaticus* habitat (Chapter 2). The low number and proportion of large females at stable rivers, therefore may reflect a lack of suitable habitat. Experimental increases in loose, unembedded rocks close to the water at five stable rivers resulted in an increase in the number of large females collected, the proportion of large females to total spiders and nests 14 months later (Chapter 2). Alongside disturbed rivers, where large areas of habitat are available the proportion of large 'female' spiders was highest, and accounted for almost 40% of the populations. Large spiders in the feeding experiment were in considerably better condition than predicted by their weight after almost two months with very little food, suggesting that by reaching large size (presumably at a slower rate) at disturbed rivers females may be buffered against periods of low food availability (see Provencher and Riechert 1991), e.g. after a flood removes benthic aquatic insects (Scrimgeour et al. 1988).

Aquatic prey abundance could have an impact on the number of juvenile spiders found at rivers across the disturbance gradient, either directly through food

limitation or indirectly through changes in the abundance or fecundity of female spiders. However, *D. aquaticus* eggsacs contain more than 300 spiderlings (M. Greenwood, unpublished data), as found in other species of *Dolomedes* (Carico 1973), and the highest population density of *D. aquaticus* reaches ~ 60 per 100 m reach. Thus, reduced female fecundity or abundance are unlikely to be limiting populations at any of the sites. Flood mortality could contribute to the low proportion of small spiders at disturbed rivers if small juveniles are more susceptible and less able to escape spates than larger individuals (e.g. Framenau and Elgar 2005). However, in general the spiders seem well adapted to avoid flood mortality as all individuals are active and mobile, females carry their eggsacs, and nests are often positioned metres from the water edge or on vegetated islands within the floodplain. Furthermore, the high abundance and proportion of small spiders found at intermediately disturbed rivers, which also experience large floods, indicates that flood mortality may not be a major contributing factor to the low abundance of small spiders at disturbed rivers.

Cannibalism and *D. aquaticus* size structure

Frequent cannibalism can have a dramatic influence on population size structure (Claessen et al. 2004) and rates of cannibalism were high at the extreme ends of my disturbance gradient. This was due to habitat limitation alongside stable rivers, combined with the changes in food availability across the disturbance gradient that led to high density, small-scale patches of spiders at both stable and very disturbed rivers (Chapter 2). The low abundance of large females at stable rivers may result because cannibalistic females that develop early in the season, and presumably at a smaller size than later developing ones (Abrams et al. 1996), could gain a reproductive advantage through removing future competitors for habitat and nest sites, a situation that can occur under intense local competition for resources (Fincke 1994, Wise 2006). High cannibalism rates at stable and disturbed rivers may also be responsible for the low abundances of juveniles at these rivers.

The tighter size distributions of *D. aquaticus* populations at stable and disturbed rivers than at intermediately disturbed sites is comparable with the reduced size variation and tightened size distributions caused by cannibalism among asynchronously hatching dragonfly larvae (Hopper et al. 1996). However, the exact effect of cannibalism on population size structure varies depending on functional and numerical responses of the cannibals (Moksnes 2004, Wise 2006), dispersal rates of

potential victims as well as the degree of resource competition between interacting cannibalistic classes (Persson et al. 2004) and their relative body sizes (Van Buskirk 1992, Benoit et al. 1998, Persson et al. 2004). To be able to understand and predict the impact of cannibalism on the population size structure of *D. aquaticus* more research will be needed to identify the specific cannibalism mechanisms operating (Moksnes 2004).

Other potential impacts on size class structure

The size class structure of populations across the disturbance gradient could also be altered by factors other than those directly associated with subsidy availability, intraguild predation rates or flood regime. *Dolomedes* spiders are more susceptible to fatal desiccation than many other spiders (Carico 1973) and desiccation stress can act as a size selective mortality factor (DeVito and Formanowicz 2003). However, *D. aquaticus* lived close to the river edge at all our sites (M. Greenwood unpub. data) so that desiccation stress should have been minimal. In addition, *D. aquaticus* often submerge themselves in water, especially when disturbed from their resting place.

Predation by extra-guild predators has the potential to alter *D. aquaticus* life history traits through size selective predation pressure. Predation attempts on *Dolomedes* by pompilid wasps (M. Greenwood pers. obs., Roble 1985), reptiles (Riley and Huchzermeyer 2000) and wading birds (in Carico 1973), among others, have been reported. However, *D. aquaticus* is largely nocturnal or crepuscular (Forster and Forster 1999) and predators of overseas species appear to be largely day active. Further research is required to investigate potential nocturnal predators in New Zealand.

Effects of cannibalism on life history traits: providing an additional food source?

Cannibalism can be a significant foraging strategy as it provides an extra food source that can facilitate the completion of larval development in time limited environments (Wissinger et al. 2004). Cannibalism may potentially prevent a population from going locally extinct, the "life-boat mechanism" (see Polis 1981), and can alleviate some of the negative effects of low alternative food sources (Moya-Larano et al. 2003, De Block and Stoks 2004). Spiders are often food limited (Henschel et al. 2001, Halaj and Wise 2002, Moya-Larano et al. 2003) and *D. aquaticus* living beside disturbed rivers might be expected to be in the poorest condition after winter, as these rivers

provide the lowest amounts of aquatic insect prey (Chapter 2). However, nearly 50% of juvenile and female spiders under eggsac-producing size had positive condition at disturbed rivers in spring, compared to 20 – 30 % at intermediately disturbed rivers despite aquatic prey abundance being similarly low at both river types. Engaging in cannibalism may provide some large spiders with an additional food source that enables them to be in better condition after winter. An increase in condition of some individuals of *D. aquaticus* through cannibalism is suggested by the coefficient of variation of the condition index of juveniles being most variable at disturbed rivers. At stable rivers, with a high abundance of aquatic prey most of the population was in 'good' condition, but at intermediately disturbed rivers where lower levels of aquatic prey were found most spiders were in 'poor' condition. At disturbed rivers successful cannibals may be able to achieve 'good' condition, whereas spiders that do not cannibalise may be in worse condition. If so, cannibalism could have significant positive effects on both the growth rate and reproductive fitness of spiders at disturbed rivers. Our experiments indicated that the condition of a spider determines the timing of the first moult after winter, with spiders in the best condition moulting almost two months earlier than those in 'poor' condition. The speed at which growth can begin with the return of warmer weather is a critical life history characteristic as it enables spiders to become sexually mature and begin reproducing sooner. Thus, the condition of spiders in spring is likely to be a critical factor determining their growth rates in summer.

Summary

Life history traits of *D. aquaticus* were driven by interactions between habitat and allocthonous prey availability, which were mediated by large-scale disturbance factors, e.g. floods. Field populations of *D. aquaticus* associated with higher amounts of allochthonous aquatic insect prey, generally did not include more large females, despite the positive effects of increased food availability on the timing of the first post-winter moult. Rather, flood disturbance, which controls the abundance of aquatic insect prey and *D. aquaticus* habitat, also alters intraspecific predatory interaction rates through changes to the small-scale spatial distribution of the spiders. Thus, disturbance appeared to have a large effect on the life history and size class structure of *D. aquaticus* by altering environmental stability, food supply, habitat availability and rates of intraspecific interactions.

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Out came the sunshine and dried up all the rain...

incy wincy spider

Chapter 5

The impact of low river flow on populations of a riparian spider

ABSTRACT

Low flows in rivers can have serious impacts on aquatic communities by changing the density of aquatic taxa, community composition and the nature and strength of biotic interactions. These effects are likely to extend into the terrestrial environment through changes to the identity and abundance of emerging aquatic prey available as prey to riparian predators. In this chapter I investigated the influence of low flows in rivers on populations of a riparian fishing spider, *D. aquaticus*, along a drying gradient in one river and in five rivers containing permanently flowing and drying reaches. The biomass of aquatic insects, potential prey for *D. aquaticus*, was lower at sites that had been dry for longer. In addition, at sites that were drying, spider biomass was lower and size classes were skewed towards more small and less large spiders. These effects were most likely caused by a combination of lower prey availability and higher desiccation stress at drying rivers. Furthermore, spider populations at reaches that had lost a large amount of wetted surface area were spatially aggregated, which when combined with the lower prey availability at these sites, may lead to higher intraguild predation, especially cannibalism. Thus, low river flow affected the biomass of *D. aquaticus* that a reach could support, as well as their size class structure and spatial distribution.

INTRODUCTION

Flow regimes have an overriding influence on the physical environment of the river channel as well as the surrounding riparian zone (Bendix 1997, Amoros and Bornette 2002). In addition, flow-related abiotic factors, such as substrate disturbance and hydrologic connectivity, often have a dominant effect on the composition and stability of aquatic communities (Winterbourn et al. 1981, Resh et al. 1988, Williams 1996, Hart and Finelli 1999, Amoros and Bornette 2002). These effects can influence the terrestrial environment by changing the abundance and identity of aquatic prey and

the suitability of the riparian zone as a habitat and foraging ground for terrestrial consumers (Chapters 2 and 3).

Although there are two main forms of disturbance influencing rivers, floods and droughts, most research has concentrated on flooding disturbance and investigations of the impacts of droughts on aquatic fauna have been largely opportunistic (Lake 2000, Lake 2003). However, the contraction of stream ecosystems can have large impacts on the in-stream biota by altering the area of habitat and physico-chemical variables such as temperature and dissolved oxygen, which often lead to changes to the nature and strength of biotic interactions (Power 1990, Power et al. 1996, Stanley et al. 1997, Lake 2003). Drought-induced changes to the composition of aquatic insect communities can alter the availability of prey to aquatic predators (Wootton et al. 1996, Marks et al. 2000) and may also change the abundance and identity of emerging aquatic insects preyed on by terrestrial predators. In addition, drought-related changes to the size structure of populations of terrestrial predators through declines in aquatic prey abundance or desiccation mortality could have significant feed-back effects on the nature of biotic interactions within the terrestrial ecosystem and across the ecotone. For example, intraguild predation rates and the size range of prey eaten by terrestrial predators may vary, potentially changing top-down impacts in both systems.

Investigation of the impact of low flows on the linkages between aquatic and terrestrial communities is critically important in light of predicted increases in the frequency and strength of droughts as global climate changes (Arnell et al. 1996) and there is increased anthropogenic pressure on water supplies.

As a river dries the amount of aquatic prey available to riparian consumers alters, potentially peaking as the river dries into pools and insects are aggregated and trapped or emerge as adults and then declining over time as the water recedes. Linkages between terrestrial floodplain and aquatic ecosystems have been hypothesised to weaken as a river dries (Boulton 2003, Lake 2003) and Gray (1993) found that densities of insectivorous birds decreased greatly in the riparian forest at those times as no insects were emerging. However, smaller consumers that cannot disperse away in search of alternative prey sources may become aggregated around drying pools. For example, Bastow et al. (2002) showed that grasshoppers consumed and congregated around algal mats stranded by receding water levels. Such short term pulses in food resource abundance can have large impacts on recipient consumers,

sometimes leading to large top-down effects (Ostfeld and Keesing 2000). In addition, as the water recedes and prey disappear, consumers must either find an alternative prey source or track the drying river. Thus in the short term, spatial aggregations of consumers around shrinking aquatic systems may lead to increased interactions between guild members and between the consumers and their aquatic prey. Moreover, for riparian consumers which are susceptible to fatal heat stress and desiccation, as are many *Dolomedes* spider species (Carico 1973), the drying of the river may also alter thermal or desiccation related mortality rates. Desiccation mortality is often size specific (Willmer et al. 2000), and once a river has dried, it could be a strong selective factor acting on population size structures. The relative effects of these mechanisms on consumer abundance, population size structure and spatial distribution will depend on the direction and frequency of stream drying, the mobility of the predatory taxa and the spatial scale of drying relative to the consumer's dispersal ability.

In this chapter I investigated the influence of river drying disturbances on populations of *D. aquaticus*, a riparian fishing spider. These spiders are likely to play an important role in the transfer of energy between aquatic and terrestrial systems by eating small emerging aquatic insects (Williams 1979) and in turn potentially being eaten by larger terrestrial predators. I studied patterns in abundance and population size structure of *D. aquaticus* along a drying gradient and between permanent and drying river reaches. *D. aquaticus* are relatively mobile and active predators and are likely to be able to track receding water levels, at least for a short time. In addition, as these spiders live under river bank rocks they will be able to utilise new habitat exposed by the receding water. I hypothesised that drying reaches would support lower spider biomass and that population size structure would vary with river permanence, due to size specific effects of desiccation stress and decreases in aquatic insect biomass. In addition, spider distributions are likely to be clumped at drying sites as they aggregate around the remaining aquatic habitat. Aggregation could have important effects on the rates of predatory intraspecific interactions as I have previously shown that high densities of *D. aquaticus* at a small-scale leads to relatively higher cannibalism rates than are found in populations that are more evenly distributed (Chapter 3).

METHODS

Longitudinal drying gradient

Five sites along the Selwyn River, South Island, New Zealand were sampled to investigate longitudinal patterns of *D. aquaticus* associated with river drying. The Selwyn River drains the central Canterbury foothills and its course extends for almost 60 km from the foothills to where it empties into Lake Ellesmere on the east coast (Larned et al. in press). Permanent flow occurs for the first 5 km below the headwaters and for 15 km above the lake inlet. However, in most months in recent years the middle 35 km of the river is dry, apart from a short reach near the confluence with the Hororata River (Larned et al. in press). The study sites used in the present study were located within this middle drying section, just upstream from the Scotts Road / Beatty Road ford (see Table 1 for site locations) and approximately 10.5 km downstream from the headwaters. This reach has an average annual flow permanence of about 90% with drying periods occurring in late summer (Datry et al. 2007).

Five sampling sites were distributed downstream from the permanently flowing reach upstream (pers. comm. S. Larned, NIWA Christchurch, New Zealand), which was designated Site 1. Site 5 was the downstream-most drying site, approximately 500 m downstream of the top site (Table 1). Specific site locations were chosen to have similar spider habitat (loose, unembedded riverbank rocks) and to provide a gradient of water permanence. All five sites were sampled three times, once while three of the five sites were dry (17 March 2006), one day after an increase in flow rewet all sites (24 March 2006) and 16 days after this (10 April 2006). Figure 1 shows Site 4 before and one day after the water returned.

Stage height and water temperature were measured every half hour using water height recorders (WHT 1000, Trutrack Ltd, Christchurch) installed in the deepest part of the channel at each site on 14 March 2006. At all sites a 20 m stretch of stream bank on each side of the river was searched for spiders (3 m wide) by systematically turning over all rocks (for more detailed survey methods see Chapters 2 and 4). All *D. aquaticus* were photographed twice on a 2 mm grid to allow size measurements to be made and spiders sexed. Male spiders were identified by their bulbous palps (Carico 1973) but I could not distinguish large juveniles from reproductively active females. However, females found with eggsacs generally have a

cephalothorax width greater than 9 mm and males mature between 5-7 mm cephalothorax width (Chapter 4). Thus non-male spiders with a cephalothorax width > 8 mm were characterised as 'female'. Spider biomass (wet weight) was calculated from a cephalothorax width: wet weight regression ($y= 0.024x^{2.69}$, $r^2=0.90$, n= 151, $p<0.001$). In addition, for the first two sampling periods, spiders at each site were marked with a small dot of acrylic paint (different colours at each site) on the abdomen and returned to the field. Spider habitat availability was quantified at each site by measuring the longest axis (l.a.) and depth of embeddedness of 50 randomly selected particles (as in Chapter 2). Depth of embeddedness was calculated as the proportion of the total depth of a rock perpendicular to the ground that was embedded in fines < 5 mm l.a. In addition, the proportion of river bank (3 m from water edge) in each 20 m reach that contained usable habitat was estimated visually in 1 m^2 blocks. Usable habitat was defined as the area that had less than 50 % of rocks over 50 mm l.a embedded in fines more than 1/5 of their depth. Furthermore, if the area had more than 50 % vegetation cover it was defined as non-usable habitat. River width was measured at 0, 5, 10, 15 and 20 metres along each study reach. This enabled the calculation of wet channel area present in the study reach in each sampling period.

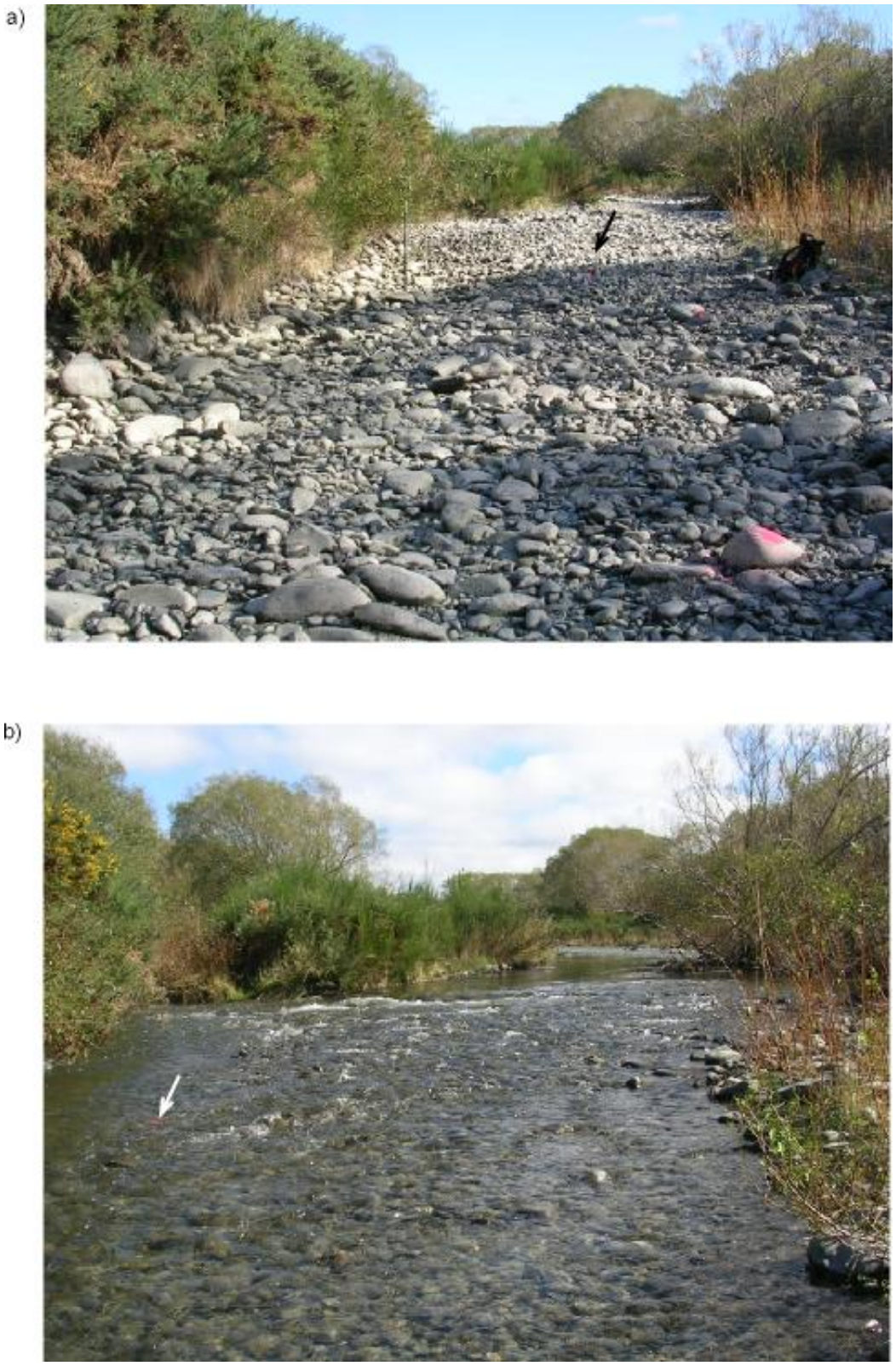

Figure 1 Site 4 on the Selwyn River (a) before (17 March 2006) and (b) one day after (24 March 2006) the entire study reach was rewetted. The second photograph is taken from a point slightly further upstream. Arrows indicate the same painted rock site marker in each photograph.

Drying vs. permanent stream sections

To investigate differences in spider populations in permanently flowing and drying stream reaches I used five replicate rivers, each with a reach that flowed all year and a reach that dried for a small proportion of the year. *D. aquaticus* are very susceptible to fatal desiccation and are generally not found in summer in areas of open river bank that have been dry for more than a few weeks (pers. obs M. Greenwood). Thus, the drying reaches were selected to be close to permanently flowing reaches and to be dry for only a few months of the year (Table 2, Figure 2). Knowledge from locals helped identify these drying reaches, which were chosen while they were still flowing. Sites 1 and 5 from the longitudinal Selwyn survey were used as the permanently flowing and drying reach, respectively. Drying sites were downstream of permanently flowing reaches at all rivers except Garry River. Each river was sampled once between October and December 2006, when all reaches were flowing, and again between February and April. The second sampling date was timed so that although water was present within the drying reach the river dried within a distance of 20 m downstream of the site. The actual sampling date depended on the drying rate of the specific river.

At each site a 20 m reach was defined, and spider sampling and measurements of habitat were conducted as described above. The distance spiders were found from the river edge was also recorded. To measure relative aquatic prey abundances I took four Surber samples (0.09 m^2, 500 μm) in riffles or runs within each site reach at the time of the second sampling. A measure of terrestrial prey availability was obtained by vacuuming five 0.25 m^2 quadrats at each site (modified auto vacuum cleaner, 12 V, 60W). Quadrats were positioned within 3 m of the river edge and all rocks within a quadrat were turned over to a depth of 5 cm. The vacuum sampler malfunctioned at the Orari River sites, thus there are no terrestrial food samples for that river. Water height and temperature loggers were positioned in the deepest part of the channel at all permanent sites. HOBO (Onset Computer Corporation) data loggers were also situated in the drying reaches. Differences in diel temperature fluctuations between the permanent and drying stream reaches and water height readings at the permanent sites at times of known low flow were used to calculate the proportion of time, and the longest interval, that the sites were dry. The proportion of the bank covered by vegetation was estimated visually.

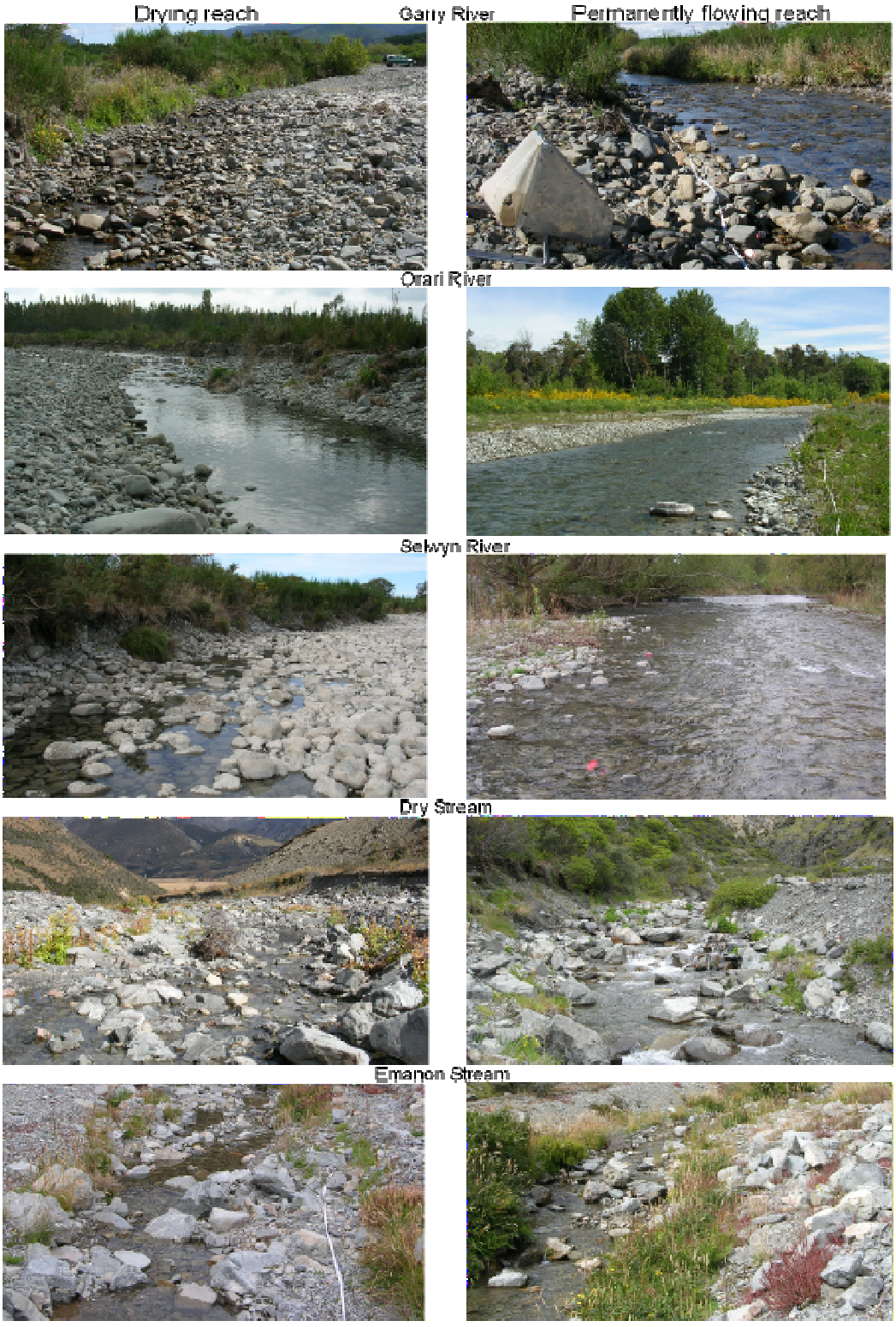

Figure 2 The permanently flowing and drying stream reaches of the five study rivers. For detailed description see Table 2.

Analyses

The small-scale densities of *D. aquaticus* can have large impacts on cannibalism rates (Chapter 3), thus I investigated patterns in spatial aggregation using the standardised Morisita index of dispersion (*Ip*) (Krebs 1998, see Chapter 3). The 20 m sampling reaches were divided into twenty one metre by three metre quadrats and the number of spiders found in each totalled. A positive *Ip* indicates a clumped distribution, while an *Ip* below zero indicates the organisms are evenly distributed. A random spatial distribution gives an *Ip* of 0 and 95 % confidence limits are ± 0.5. The relationship between the area of wetted channel and the spatial distribution of spiders in the longitudinal Selwyn River survey was tested using regression analysis. Data from the first two sampling dates were used to include a wide range of wetted areas.

Drying vs. permanently flowing reaches

To test the effects of site permanence on spider biomass I performed ANOVAs using the river term as a block. This allowed me to test the hypothesis that there would be no effect of site type at time one when all reaches were flowing. At time two, when low flow occurred at the drying reaches, it was expected that differences between sites would occur. The proportions of small and large spiders were tested the same way using MANOVAs. Regression analysis was used to test the effects of the longest interval in the preceding month that a drying site lacked flow against the dry weight of aquatic insects found at that site. The spatial distribution patterns of spiders at sites where the river contracted by more than half its width versus those where the river remained relatively similar in area were conducted using ANOVA with site as a predictor and river as a block. A contraction of 50% width or more was chosen arbitrarily to designate a major disturbance. Since low flow can be regarded as a 'stepped disturbance' (Boulton 2003) this categorical treatment is appropriate. All analyses were performed in Statistica version 6 (Statsoft Inc. 2003) and data were log or arcsine square-root transformed to meet assumptions of normality and heteroscedasticity.

RESULTS

Longitudinal drying patterns

The permanently flowing upstream site on the Selwyn River, Site 1, retained water for the entire sampling period and the proportion of time a site was wet for (over the two weeks prior to the water returning) decreased with distance downstream (Table 1). During a high flow on 23 March, when the water returned to all study sites on the Selwyn River, minimal movement of *D. aquaticus* riverbank habitat occurred and the water remained in the same channel. Mean substrate size and the proportion of usable *D. aquaticus* habitat were similar at all sites (Table 1).

Table 1 Physical characteristics of riparian sampling sites (20 m reaches) along a drying gradient in the Selwyn River, Canterbury. Site 1 is the upstream permanently flowing site. The proportion of usable habitat was measured visually over the 20 m reach and is defined as the area of riparian strip with less than 50 % of rocks over 50 mm longest axis embedded in fines more than 1/5 their depth. The proportion of time that surface water was present was measured in 10 min intervals over the 16 days before the entire reach was rewet. Width dry, 1 day rewet and 16 days rewet are the mean widths of the river at each site on 17 and 24 March and 10 April, respectively.

Site no.	Cumulative distance (m) between sites	% usable habitat	Mean ± 1 SE substrate size (mm)	% time with water	Width dry (m)	Width 1 day rewet (m)	Width 16 days rewet (m)
1	0	38	147 ± 13	100.0	5.8	7.7	7.5
2	272	48	152 ± 14	33.0	2.4	11.8	10.6
3	341	43	165 ± 14	6.3	-	11.7	10.9
4	396	30	144 ± 12	6.1	-	7.3	7.0
5	549	55	166 ± 13	2.8	-	7.2	6.9

Spider biomass, spatial distribution and the proportions of small and large spiders all showed distinct differences among sites when the downstream section of the river was dry. However, the differences then disappeared or were markedly smaller once the water returned to all sites (Figure 3). Initially, when Sites 4 and 5 were dry, spider biomass was much higher at the sites with flowing water (1, 2 and 3) and decreased in a downstream direction (Figure 3a). However, two weeks after the water returned spider biomass was more evenly distributed across the sites, and in fact the highest biomass was found downstream of previously dry sites (Figure 3a). No spiders were found at the furthest downstream dry site (Site 5) on the first sampling occasion. Spider numbers showed similar patterns to spider biomass.

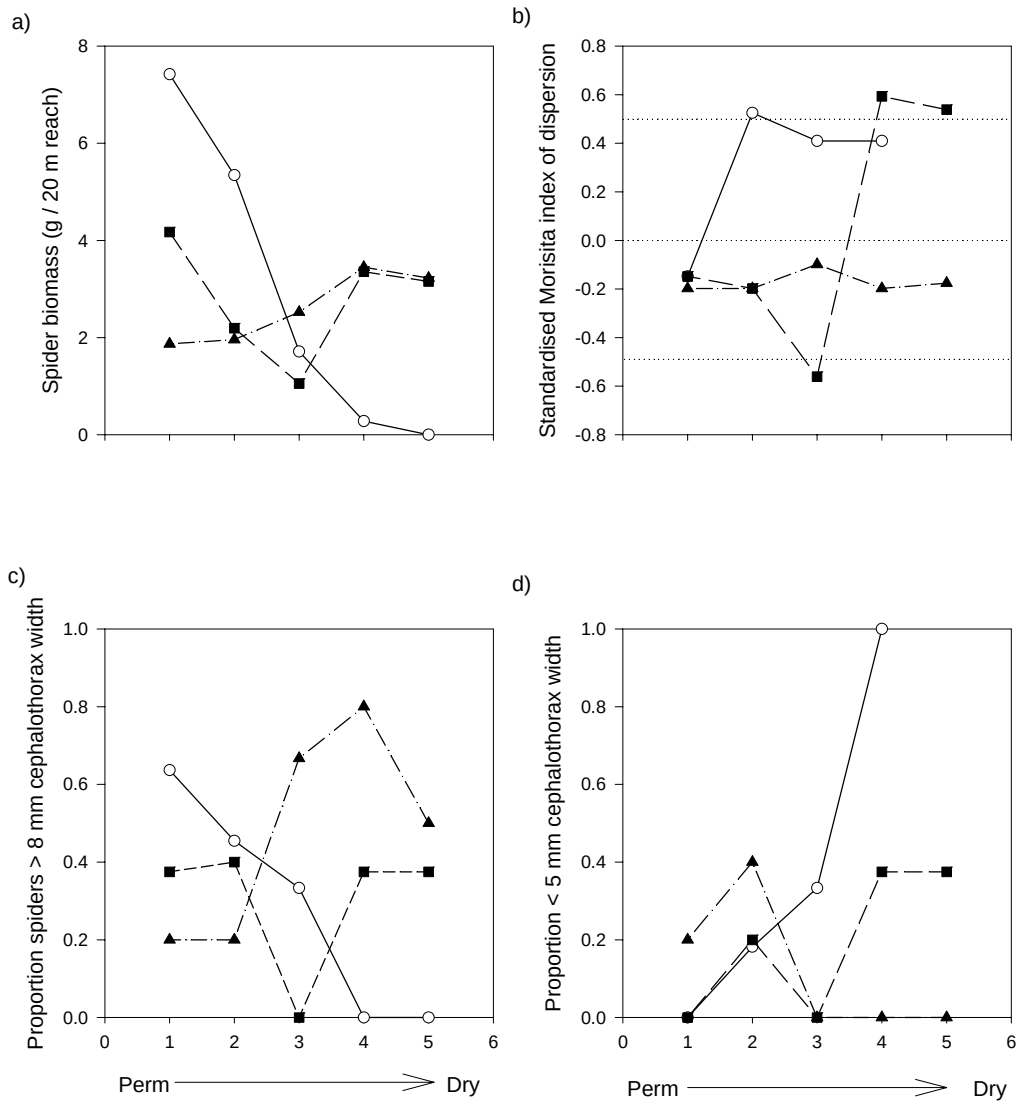

Figure 3 (a) *D. aquaticus* biomass, (b) standardised Morisita index of dispersion, and (c) proportions > 8 mm and (d) < 5 mm cephalothorax width spiders in 20 m reaches at five sites along the drying Selwyn River when the river had been dry all summer (open circles), one day after the river rewet (filled squares) and 16 days after rewetting (filled triangles). Sites 4 and 5 were dry during summer sampling (17 February 2006) and the entire reach was rewetted on the 23 March 2006. The standardised Morisita index of dispersion ranges from 1.0 to -1.0; random patterns give an index score of zero, clumped patterns above zero and uniform patterns below zero. Dotted lines indicate 95 % confidence limits.

When it was dry on 17 March *D. aquaticus* spiders were spatially aggregated at a small scale at all but the most permanently flowing site (Figure 3b). However, when the water returned a week later spiders were only clumped at the two most downstream sites, and after a further two weeks they were randomly distributed at all sites (Figure 3b). The clumping patterns of *D. aquaticus* showed a trend towards more aggregation where the area of wet channel was lower (Figure 4, $F_{1, 7} = 5.10$, $r^2 = 0.43$, $p = 0.06$).

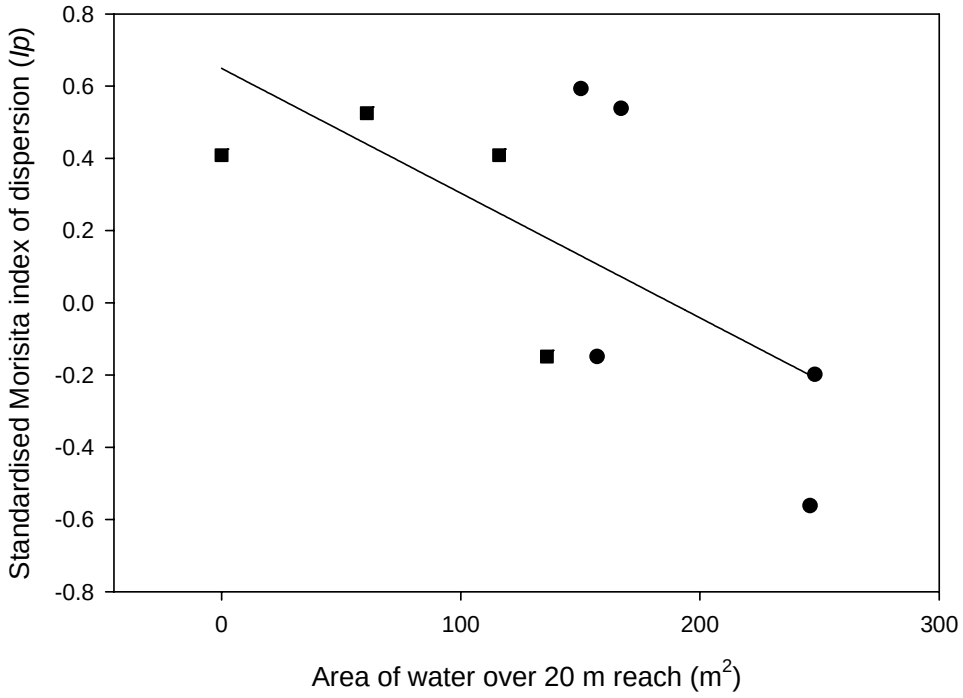

Figure 4 Dispersion of *D. aquaticus* spiders at each site as indicated by Morisita's index of dispersion in relation to the area of wetted channel (m^2) in a 20 m reach. Data have been combined from before the rewetting of the channel (17 March, filled squares) and one day after the channel became rewetted (24 March, filled circles).

No large spiders (> 8 mm cephalothorax width) were found at the two driest sites during the first sampling period, while more than half the spiders at the most permanent site were large (Figure 3c). However, two weeks after rewetting at all sites the previously dry sites mainly supported large spiders (50 – 80%), whereas few occurred at the upstream, permanent site (Figure 3c). On all three sampling dates numbers of large female spiders and their proportion in the population showed the

same pattern. Low numbers of small spiders were found in all three sampling periods and no obvious pattern was observed in the number of small spiders across the drying gradient on the different dates. However, the proportion of spiders that were small showed different patterns when the river was dry to when it had rewet. During the first sampling period all spiders found at the downstream dry sites were small, while no small spiders occurred at the most permanent site (Figure 3d). However, one day after the flood fewer small spiders occurred at the dry site and two weeks after rewetting, the previous pattern had almost been reversed with no small spiders at dry sites but some present at the permanent reach (Fig 3d).

Of the 71 spiders marked on first two sampling trips only three were subsequently found. Two spiders had moved from their previous sites and one was found again at the same site. This is insufficient evidence to draw any conclusions about movement patterns of *D. aquaticus.*

Drying vs. permanently flowing stream reaches

Drying patterns

Permanently flowing reaches on the five rivers retained high levels of flow throughout the summer (Table 2) whereas all drying sections had lost surface flow to within at least 20 m of the sampling site location. Due to a relatively wet summer, most drying sites had low flows for a comparatively short time before being sampled. The proportion of time between the two sampling dates that the drying sites contained water ranged from 85 to 99% (Table 2). Four of the rivers dried upstream in a relatively gradual manner, however the dry reach in Dry Stream fluctuated in degree of wetness and rewet approximately nine times between the two sampling dates (Table 2). Unfortunately the temperature logger in the Orari River was stolen, so I do not know how long the drying reach of this river was dry. However, the daily river flow data on the Environment Canterbury web site (www.ecan.govt.nz / Our + Environment / Water / Rivers / RiverFlows) with concurrent gauging runs down the river confirmed that the permanently flowing reach retained water for the entire study period.

Table 2 Physical characteristics of study sites on five rivers, each with a permanently flowing and a drying reach. Permanent sites are upstream of drying sites except on Garry River. The logger was stolen from the Orari River, so there are no drying data (N/A). Grid references refer to Infomap 260 published by the Department of Survey and Land Information, New Zealand. Mean terrestrial insect biomass at each reach is shown with ± 1 se.

River	Site	Grid ref.	Mean substrate size (mm ± se)	% time wet	No. times rewet	Width time 1 (m)	Width time 2 (m)	Terrestrial insect biomass (mg dw/m^2)
Orari River†	Perm	J37:687891	109 ± 10	NA	NA	8.4	6.4	NA
	Dry	J37:696875	116 ± 12	NA	NA	7.4	3.4	NA
Garry River	Perm	M34:569756	106 ± 10	100	-	7.0	5.2	11 ± 2
	Dry	M34:554773	109 ± 9	99	0	7.8	1.9	62 ± 9
Selwyn River	Perm	L35:272450	157 ± 16	100	-	10.0	9.2	53 ± 6
	Dry	L35:275445	167 ± 14	87	1	5.9	3.4	77 ± 9
Dry Stream	Perm	K34:063710	155 ± 23	100	-	3.8	3.1	14 ± 1
	Dry	K34:060711	154 ± 19	85	9	3.0	1.4	41 ± 7
Emanon	Perm	K35:060677	120 ± 17	100	-	1.9	1.7	206 ± 28
Stream*	Dry	K35:059677	142 ± 20	98	1	1.6	1.0	49 ± 10

* unofficial name
† logger missing

Habitat and food availability

Habitat available to *D. aquaticus* varied between rivers but did not differ consistently between permanent and drying reaches. Substrate size varied between rivers ($F_{4, 4}$ = 126.3, p = <0.001) but not sites ($F_{1, 4}$ = 4.22, p = 0.11, Table 2). The coefficient of variation of substrate size showed a similar pattern (river: $F_{4, 3}$ = 9.32, p = 0.05, site: $F_{1, 3}$ = 0.50, p = 0.53) and the proportion of unembedded rocks over 50 mm longest axis did not differ significantly between rivers or sites (river: $F_{3, 4}$ = 1.26, p = 0.44, site $F_{1, 3}$ = 0.07, p = 0.81).

Terrestrial prey abundance did not differ between permanently flowing and drying stream sections ($F_{1, 3}$ = 0.083, p = 0.79, Table 2). But after the rivers had begun to dry aquatic invertebrate biomass was significantly lower in drying stream sections than in those that were still permanently flowing (Figure 6a, $F_{1, 4}$ = 14.34, p = 0.02). The difference in aquatic invertebrate biomass between permanently flowing and drying reaches was significantly and positively related to the longest interval of drying during the preceding month (Figure 5, $F_{1, 3}$ =18.5, p = 0.05, r^2 = 0.90). Thus,

when a reach had been dry for a longer period of time there was a greater difference between the permanently and intermittently flowing reaches in the abundance of aquatic insects.

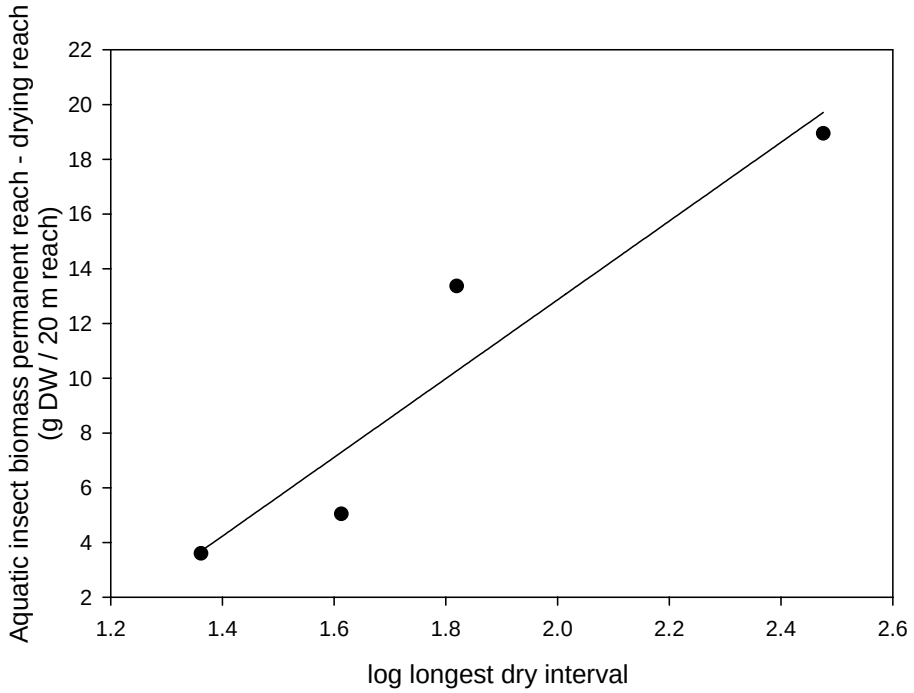

Figure 5 Biomass of aquatic insects (g DW per 20 m reach) in the drying reach of four rivers and the longest interval the reach has been dry in the preceding six weeks ($\log_e$ transformed). Aquatic insect abundance is shown relative to the permanently flowing reach sampled in each river. The relationship is described by: aquatic food = -15.9 + 14.38* $\log_e$ dry interval length, for statistics refer to results section.

When all river sections were permanently flowing *D. aquaticus* biomass ($F_{1, 4}$ = 0.09, p = 0.8), and the proportion of both small (< 5 mm cephalothorax width) and large (> 8 mm cephalothorax width) (MANOVA multivariate site; Wilks $\lambda_{2, 3}$ = 1.01, p = 0.46) spiders did not differ significantly between stream sections (Fig 6 b, d, & f). However, in late summer when the drying sections had begun to dry, rivers had a significant effect on the proportion of large and small spiders (MANOVA river; Wilks $\lambda_{8, 6}$ = 4.96, P = 0.03). This effect was driven by differences between rivers in the proportion of small spiders (MANOVA univariate river; $F_{4, 4}$ = 14.37, p = 0.01). In addition, a significant multivariate effect of site was found (site; Wilks $\lambda_{2, 3}$ = 12.63, p

= 0.03), and was brought about by fewer large spiders and more small juveniles at drying sites (MANOVA univariate site large spiders; $F_{1, 4} = 9.89$, $p = 0.03$, small spiders; $F_{1, 4} = 32.73$, 0.005, Figure 6 e & g). There was no significant difference in spider biomass between sections ($F_{1, 4} = 4.81$, $p = 0.09$) but there was a significant biomass difference between rivers ($F_{4, 4} = 13.53$, $p = 0.01$, Figure 6c). Four of the five rivers had higher biomass in the permanent section than the drying section when the rivers were drying, although a power analysis indicated there was a 55 % chance of making a type II error at $\alpha = 0.05$, due to large variation among rivers ($1- \beta = 0.45$).

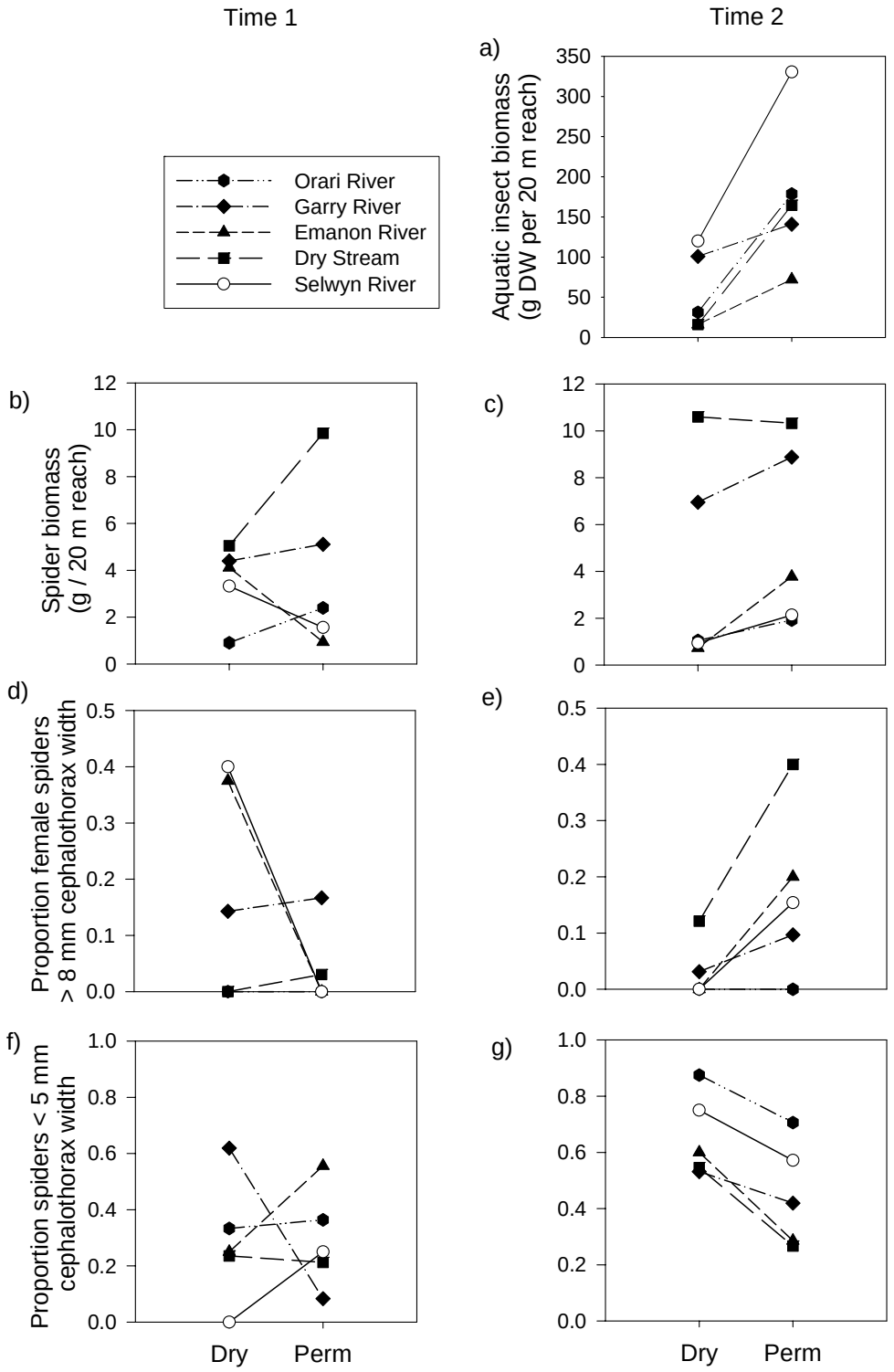

Figure 6 (a) The dry weight of aquatic insect taxa with a winged adult stage in drying (dry) and permanent (perm) sections of five Canterbury rivers in late summer when the drying sections were almost dry (Time 2). The (b, c) biomass and (d, e) proportion of *D. aquaticus* spiders larger than 8 mm and (f, g) smaller than 5 mm cephalothorax width in intermittent and permanently flowing stream sections at Times 1 and 2, respectively. All sites were flowing at time 1 (October to December) and drying sites were almost dry at all rivers at time 2 (March-April).

The standardised Morisita index of dispersion was higher for *D. aquaticus* in rivers that had decreased in width by at least half compared to those that had not. Thus spider populations at sites where the river had shrunk substantially were spatially aggregated at a small scale (two sample t-test, $t = 7.45$, $p_{2,\ 0.05} = 0.017$, Figure 7).

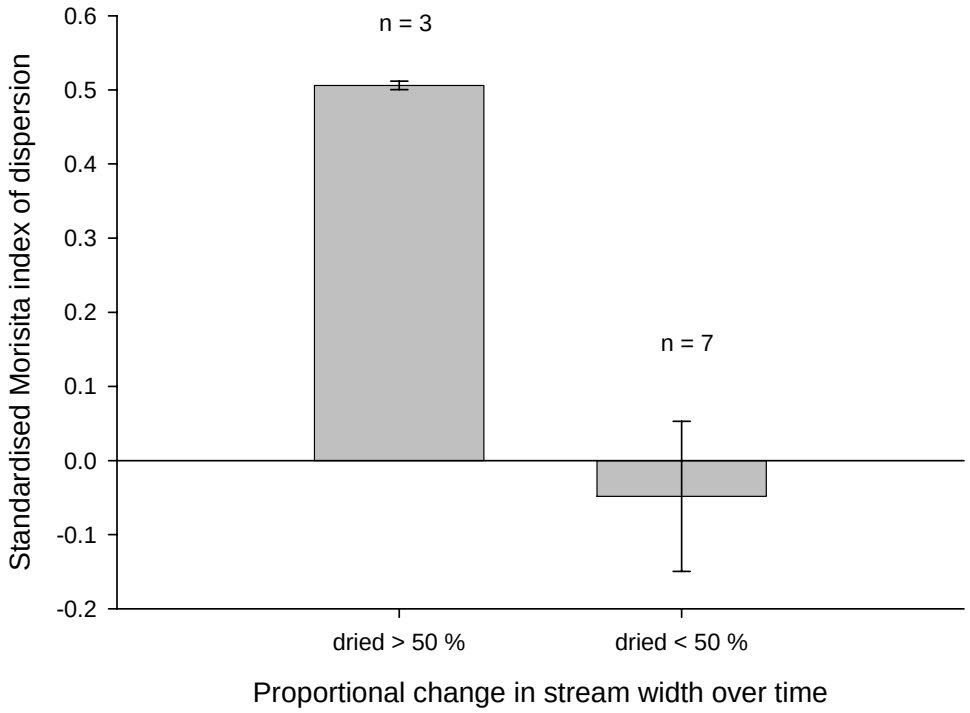

Figure 7 Dispersion of *D. aquaticus* in reaches that dried by more and less than half their widths between October - December 2006 and March - April 2007 indicated by the Morisita index (mean ± 1 S.E.).

DISCUSSION

The abundance and biomass of terrestrial consumers that a river reach can support is often related to the productivity of the aquatic system (Burdon 2004). Although drying rivers may have a high biomass of aquatic insects early in the drying process as organisms are trapped and concentrated by the decreasing water levels (e.g. Stanley et al. 1994, Dewson et al. 2007) this will be a short term effect if drying continues (Lake 2003). The overall productivity of a river often declines as the area of aquatic habitat decreases with receding water level (Stanley et al. 1997) and can lead to a decrease in the number and biomass of emerging aquatic insects available as prey to riparian consumers (Gray 1993). In my five drying rivers the dry weight of aquatic insects was lower in drying than permanently flowing reaches and the maximum length of time that a reach had been dry in the month preceding sampling was negatively correlated with the biomass of aquatic insect larvae present at a site (relative to the biomass at the permanent site in the river). Terrestrial insect biomass did not differ between drying and permanently flowing river reaches. Thus lower aquatic prey levels may contribute to the lower biomass of spiders found in drying reaches as observed in short-term experiments in which aquatic insect subsidies to riparian spiders have been reduced (e.g. Paetzold et al. 2005, Marczak and Richardson 2007).

Although overall production of a river may decline during a drought, isolated pools can become temporary hotspots of production (Lake 2003) as increasing temperatures stimulate algal growth and mobile aquatic taxa become concentrated (Stanley et al. 1997). Subsequently increased movement and emergence rates of stranded or low-flow stressed insects (Wiley and Kohler 1979, Delucchi 1989) could increase their availability to fishing spiders as prey. For example, water temperature can alter the presence of top down cascades in a three trophic level system by changing movement and feeding rates of fish and grazers and by altering algal growth rates (Kishi et al. 2005). Furthermore, if dissolved oxygen concentration falls aquatic prey may increase their movement rates or (if air breathing) surface more often, increasing their vulnerability to attack by *Dolomedes*, which hunts at the water surface (Moore and Townsend 1998). Conditions found in drying stream reaches can also speed up growth and/or development rates of some aquatic organisms (Anderson et al. 2001), potentially allowing them to escape as adults before the river dries

(Denver et al. 1998, Peckarsky et al. 2000) but see (Delucchi and Peckarsky 1989). Such behaviour may result in short-term increases in the availability of winged aquatic insects as prey for riparian predators. Overseas mayflies are able to emerge early in response to increases in predation pressure or water temperature (Peckarsky et al. 2002, Harper and Peckarsky 2006), however no conclusive evidence exists for New Zealand mayflies. However, even if they can emerge early in response to drying conditions mayflies might not be as available as prey to *D. aquaticus* as other taxa. Caddisflies and stoneflies, which crawl to the water's edge to emerge and often remain as adults within the riverbank habitat of the spiders (Paetzold et al. 2006) may be more available. Drying and permanent river sections did not differ markedly in biomass of the main aquatic insect orders (M. Greenwood unpub. data). Thus, drying is unlikely to change the kinds of aquatic insect prey available to *D. aquaticus*, at least until very little surface water is present.

Brief pulses of increased aquatic insect prey emergence associated with flow reduction may affect consumer populations, depending on the length and frequency of the pulses (Ostfeld and Keesing 2000) and the consumer's feeding preferences and dispersal ability relative to the scale of drying (Stanley et al. 1997). *D. aquaticus* is likely to be able to respond to short term increases in aquatic insect emergence as it is relatively mobile and can use the increased river bank habitat exposed by the declining water level. However, long term survival of the spiders will be determined by the rate and constancy of drying. Thus, whether the spiders keep pace with the drying tongue is an interesting question. Because the spatial distribution and size class structure of *D. aquaticus* in the Selwyn River changed one day after the river rewet, it appears that spiders are able to respond quickly to changes in flow. In contrast, responses to stream drying may be slower and it seems likely that spiders in the Selwyn took advantage of the river current to disperse downstream from sites with permanent flow. In drying rivers spiders would have to keep pace by moving upstream (if that is the direction of drying). In general, spiders in drying sections are likely to be food-limited in the long term (weeks to months) as the spatial extent of drying is likely to exceed their dispersal ability. In addition, costs associated with increased movement and foraging rates may mean that riparian consumers cannot respond fully to the short temporal peak in emergence if such activity exposes them to increased risk of desiccation or predation by other predators aggregating around the shrinking stream (Abrams 1991).

The general decline in aquatic invertebrate biomass (and by implication, food availability) in drying rivers would be predicted to have an impact on the size structure of *D. aquaticus* populations. Large individuals should be able to survive longer under food stress (Chapter 4) unless the nature of the food available changes to a (smaller) prey type that favours smaller spiders. Variation in susceptibility to thermal/desiccation stress may also contribute to the differences in *D. aquaticus* biomass and population size structure seen in drying and permanent reaches as smaller spiders have larger body surface area to volume ratios, which can alter thermal/desiccation tolerance (Willmer et al. 2000). To resist desiccation, many riparian spiders depend on the high soil moisture levels found near the river (Carico 1973, DeVito and Formanowicz 2003). Because temperature in the riverbank rock habitat of *D. aquaticus* can reach very high temperatures in summer *D. aquaticus* is likely to be particularly dependent on damp environments close to the river edge. Juveniles of *Pirata sedentarius*, a cursorial, riparian spider survived thermal/ desiccation stress longer than larger bodied adults (DeVito and Formanowicz 2003). This suggests that this type of stress could help to account for the lower population size and decreased abundance of large *D. aquaticus* observed at drying rivers. Reduced availability of prey should lessen the likelihood of small individuals surviving at drying sites (Chapter 4), the opposite pattern to that observed, suggesting that desiccation and/or thermal stress may cause the size class differences observed between drying and permanently flowing river sites. However, at all sites flowing water was still present within the river channel and *D. aquaticus* is often observed submerged underwater. This would be the best method to avoid desiccation. Both thermal/desiccation mortality and prey limitation are likely to act synergistically to alter size specific mortality rates at drying rivers. For example, thermal/desiccation stress can be related to time since last meal since this affects the size of the abdomen and the amount of water currently stored in the body (DeVito and Formanowicz 2003, Chapter 4). Size selective predation of large *D. aquaticus* by other predators congregating around the drying pools of the river may also lead to low proportion and number of these spiders found at drying reaches.

The small-scale (3 m^2) spatial distribution of *D. aquaticus* became aggregated when the surface area of wet channel was low but at all other times spiders were distributed more evenly. This might indicate a cost is associated with high small-scale densities, such as the likelihood of increased cannibalism rates at highly flood-prone

rivers, where aquatic prey abundance is low and spider populations are aggregated (Chapter 3). High cannibalism rates have the potential to have large effects on the size class structure of populations (Claessen et al. 2004). Although if this were the case large *D. aquaticus* could be expected to predominate at drying sites as they are likely to have a body size advantage in cannibalistic encounters (Dong and Polis 1992). However this was not the case.

Lastly, although the same patterns of biomass and size class structure of *D. aquaticus* occurred between sites when the rivers began to dry there were still large differences between rivers. These differences could be influenced by the direction, timing, predictability and length of previous dry periods (Williams 1996, Stanley et al. 1997, Wissinger 1999, Lake 2003), as well as the length of time that consumers are exposed to desiccation stress. Sites that dry and rewet may support a higher abundance or biomass of invertebrates than sites that dry more rapidly. Whiles and Goldowitz (2001) found that wetlands of intermediate hydroperiod had the highest insect emergence and production, as drying mortality and fish predation limited insect abundance in the drier and more permanent sites, respectively. Dry Stream dried and rewet nine times in the month preceding the drying samples, whereas the other rivers dried more evenly and gradually at this time, and although standing biomass of aquatic food was very low in the drying section of Dry Stream it supported a higher *D. aquaticus* biomass in the drying reach than the other rivers. The biomass difference between the permanent and drying reach was slight and this may indicate that periodic rewetting reduces heat/desiccation mortality of spiders, and that aquatic prey abundance was not limiting their populations, at least during that month.

Predicted alterations to global climate patterns, including an increased occurrence of droughts in many areas (Arnell et al. 1996), means that understanding the impact of river low flows on adjacent ecosystems is of considerable importance (e.g., Harper and Peckarsky 2006). The drying of rivers has serious consequences, not only for the aquatic organisms inhabiting them, but also for the abundance and biomass of terrestrial consumers that are supported (at least in part) by the river reach. The nature of the drying regime, the relative dependency of the consumer on aquatic subsidies and its scale of dispersal relative to the scale of drying will largely determine specific consumer responses and merits more investigation. The changes in population size and size class structure of *D. aquaticus* I found at river reaches that flowed permanently or had lowering flow were likely related to a reduction in aquatic

prey abundance and an increase in thermal/desiccation threat as the river dried. Furthermore, the combination of aggregated spider distributions and low aquatic food availability seems to provide ideal conditions for increased predatory interactions between conspecifics.

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Chapter Six

General Discussion

This chapter summarises the findings from previous chapters and draws general conclusions about the impact of cross-ecosystem subsidies of prey on predator populations.

Ecological research deals with understanding how organisms interact with each other and their environment, and with investigating the determinants of population and community structure (Agrawal et al. 2007). Incorporating the landscape setting into ecological research, particularly food web studies, has recently become a major focus (e.g., Polis et al. 2004). This approach has revealed that flows of nutrients and organisms between ecosystems and habitats can have large impacts on the food web structure of recipient communities. Most research dealing with transfers of energy between ecosystems has either highlighted the strong top-down or bottom-up effects that such energy transfers can have (Nakano and Murakami 2000, Sabo and Power 2002a, Knight et al. 2005, Rand et al. 2006), or has developed theoretical predictions for when subsidies may impact recipient communities (Huxel and McCann 1998, Huxel et al. 2002, McCann et al. 2005). There have been few empirical tests of theoretical principles (e.g., Polis and Hurd 1995, Iwata et al. 2003, Marczak et al. 2007a). Moreover, the role of landscape setting in determining the magnitude, direction and importance to consumers of spatial prey transfers between ecosystems has been identified repeatedly as needing more empirical research (Polis et al. 2004, Baxter et al. 2005). To predict when strong linkages occur between ecosystems we need to investigate the relative importance of multiple interacting processes and the factors that constrain responses to cross-ecosystem subsidies (Power et al. 2004, Agrawal et al. 2007). The best examples so far are Polis et al. (1998) and Anderson and Polis (2004) studies documenting how inter-annual weather patterns, densities of predators and nutrient deposition via sea bird guano interacted differently on islands of varying sizes in the Gulf of California to determine the abundances of spiders.

Island size was important as small islands received more marine algae and more carcasses washed ashore per unit island area.

Some of the largest effects of spatial subsidies of prey on recipient taxa and communities have been reported from bare cobble bar habitats adjacent to productive rivers (Marczak et al. 2007a). Many riparian predators (e.g., spiders, beetles and lizards) inhabit these bars, depend on emerging aquatic insects for a significant component of their diet, (Hering and Platcher 1997, Sabo and Power 2002b, Paetzold et al. 2005), and can play important roles in determining terrestrial community structure (e.g. Henschel et al. 2001). Often the densities of these predators are related to the productivity of aquatic systems as more productive aquatic habitats provide higher levels of emerging insects for terrestrial predators (Burdon 2004, Power et al. 2004).

River flow regimes are one of the most important factors influencing the standing biomass and secondary production of aquatic systems (Gray 1993, Digby 1999, Chadwick and Huryn 2007), especially in unshaded rivers (Death and Zimmermann 2005) like those studied in this thesis, and are likely to have a large effect on the abundance of terrestrial consumers a reach can support. Flow regimes also change the nature of the riparian vegetation (Bendix 1997). Since the permeability of the ecosystem boundary to the movement of subsidies often determines their effects (Polis et al. 1997, Cadenasso et al. 2004, Huxel et al. 2004) alterations to riparian conditions will be important. For riparian predators (such as waterstriders and fishing spiders) that feed on emerging insects right at the land-water boundary, ecotone permeability to adult aquatic insects is not likely to be a major influence. However, physical changes to the riparian zone through effects of flooding may affect populations of these terrestrial consumers by altering the suitability of the area as a habitat or foraging area (Ballinger et al. 2005), potentially changing the availability of aquatic subsidies to particular terrestrial predators as well as their ability to respond to such subsidies.

In this thesis I demonstrated how environmental gradients related to river flow regimes controlled both the magnitude of potential cross-ecosystem prey subsidies (aquatic insects) available to a riparian spider predator, *Dolomedes aquaticus*, and mediated it's response by changing the physical nature of the riparian zone. By studying one predator species across a range of environmental conditions I investigated the relative importance of multiple factors, elucidating conditions in

which cross-ecosystem prey subsidies are particularly important for determining the spider's population size and structure.

D. aquaticus spiders live under a wide variety of river flow regimes, provided loose riverbank rocks are present as habitat (Williams 1979, Forster and Forster 1999) and the channel remains wet during most months (M. Greenwood, pers obs.). They hunt on the water surface from riverbank rocks, eat mainly aquatic insects (Williams 1979, Collier et al. 2002) and are mobile, cursorial predators that are likely to be able to track small-scale changes in prey and habitat availability.

The relative importance of habitat and aquatic prey abundance, flow-related mortality and intraguild interactions on populations of *D. aquaticus* in rivers that vary in flood or drying disturbance is summarized in Table 1 and Figure 1. The impact of each factor was judged to be high if it was likely to affect *D. aquaticus* population size, population size class structure or life history traits.

Table 1 The relative importance of variables influencing *D. aquaticus* population size, population size structure or life history traits in different environmental conditions. Evidence from surveys, experimental manipulation* and stable isotope analysis†. Flow related mortality is inferred from observations. The impact of predators on *D. aquaticus* is not included as the spiders are nocturnal and little is known about the distribution of potential predators. Rivers that have dried are only included for the section of time just after they dry because if the water disappears for more than several weeks, *D. aquaticus* spiders are not found at the site.

River flow regime	Riparian habitat limitation	Aquatic Prey	Flow-related mortality	Intraguild interactions
Flood-prone	✗?	✓	✗?	✓*†
Intermediate	✗	✓	✗?	✗*†
Stable flow	✓*	✗	✗	✓ *†
Drying	✗	✓	✗	✓ ‡
Dry	✗	-	✓	✓ ‡

‡Stable isotope samples from drying sites are being processed currently.

Habitat availability increased at more flood-disturbed rivers as scouring floods create and maintain the loose riverbank rock habitat used by *D. aquaticus* (Chapter 2). Less flood-prone, stable rivers had the only sites at which habitat limitation made a large impact on populations of *D. aquaticus* (Chapter 2, Table 1). All sites studied

that flooded had unconstrained flood plains, and drying sites also had largely open, unvegetated riverbanks. *D. aquaticus* populations were two to three times lower at stable and highly flood-prone rivers than in more intermediately flood-disturbed rivers (Chapter 2). When habitat availability was increased within a 20 m^2 reach at stable rivers *D. aquaticus* population size doubled and the number of large females also increased markedly (Chapter 2). Stable vegetated islands close to the water's edge seem to be preferred by spiders at disturbed rivers and may be limiting at these sites also.

Mortality effects related to the river flow regime are likely to be higher in drying rivers than those that flood (Table 1, Figure 1). *D. aquaticus* is well adapted to avoiding the rolling rocks and high water levels associated with floods, however the spiders are very desiccation prone (M Greenwood pers. obs.) and size-selective mortality is likely to have a large impact on their populations once the rivers dry (Chapter 5). However, while the channel remains wet the lower biomass of aquatic insect prey in drying river sections probably caused the lower population sizes and smaller proportion of large spiders found at drying sites compared to reaches than remained permanently flowing (Chapter 5). Due to the unpredictable nature of floods in many of New Zealand's rivers (Winterbourn et al. 1981) life history traits of *D. aquaticus* are unlikely to vary in response to flood frequency or timing (Lytle 2001). However, river drying is more seasonal and predictable in some eastern lowland New Zealand rivers (e.g., Larned et al. in press) and may have a greater effect on life history traits in these rivers than flood disturbance.

The combined influences of habitat and aquatic prey availability led to small-scale high densities of *D. aquaticus* at sites on stable and disturbed rivers, due to patchy spatial distribution of these two resources. Cannibalism, a specific form of intraguild predation, was higher at these sites and was most likely driven by spider density differences, although prey availability influenced weight gain of cannibals in an experimental manipulation (Chapter 3). The different relative rates of cannibalism probably had the most effect on the size and size class structure of *D. aquaticus* populations at the extreme ends of the flood disturbance gradient (Chapter 4, Table 1). Stable isotope samples were collected to investigate patterns in *D. aquaticus* diet (i.e., the relative importance of aquatic and terrestrial prey sources) and the extent of cannibalism in drying and permanently flowing stream sections. Unfortunately, these samples were not analysed in time to be included in this thesis but will be

incorporated in papers submitted for publication. It is likely that increased density-dependent processes will occur as consumers respond numerically to subsidies of prey (Huxel et al. 2004). Furthermore, predation and competition between terrestrial consumers of emerging aquatic insects is likely to be high as rivers dry (Table 1), because many predatory taxa, including *D. aquaticus* (Chapter 5), congregate around drying waterbodies (e.g., Gonzalez 1996).

The biomass of larval aquatic insects with a winged adult stage was affected by the flow disturbance regime and was highest in rivers that are stable and that retained permanent flow. The abundance of aquatic insects is likely to have major effects on *D. aquaticus* populations at all rivers except the least flood-prone ones, where habitat limitation prevents responses (Chapter 2) and at rivers that are dry, where aquatic insects are largely non-existent and desiccation stress is high (Table 1). Thus, aquatic subsidies played an important role in altering population size (Chapters 2 and 5), size class structure (Chapters 2, 4 and 5) and cannibalism rates (Chapter 3) of *D. aquaticus* populations across the flow-related environmental gradients of my study sites. However, the potential effects of aquatic prey abundance was altered and in some cases negated (e.g., at stable rivers) by other factors that were also controlled by the flow regime of the river. These additional factors included habitat availability, feeding preferences of the focal consumer, and competitive and predatory encounters with intraguild predators. In addition, effects of habitat and aquatic prey availability on *D. aquaticus* population size, size class structure and life history traits are likely to be non-additive, due to variations in cannibalism rates across the flood disturbance gradient (Figure 1). Thus, to predict effects of cross-ecosystem subsidies the particular habitat requirements of the focal species must be included, a task that becomes complex when entire communities are being investigated. My study of *D. aquaticus* highlights the need, identified previously by Power et al. (2004), to investigate the factors that constrain or modify a species response to cross-ecosystem subsidies, in addition to studying what alters the magnitude of the subsidy.

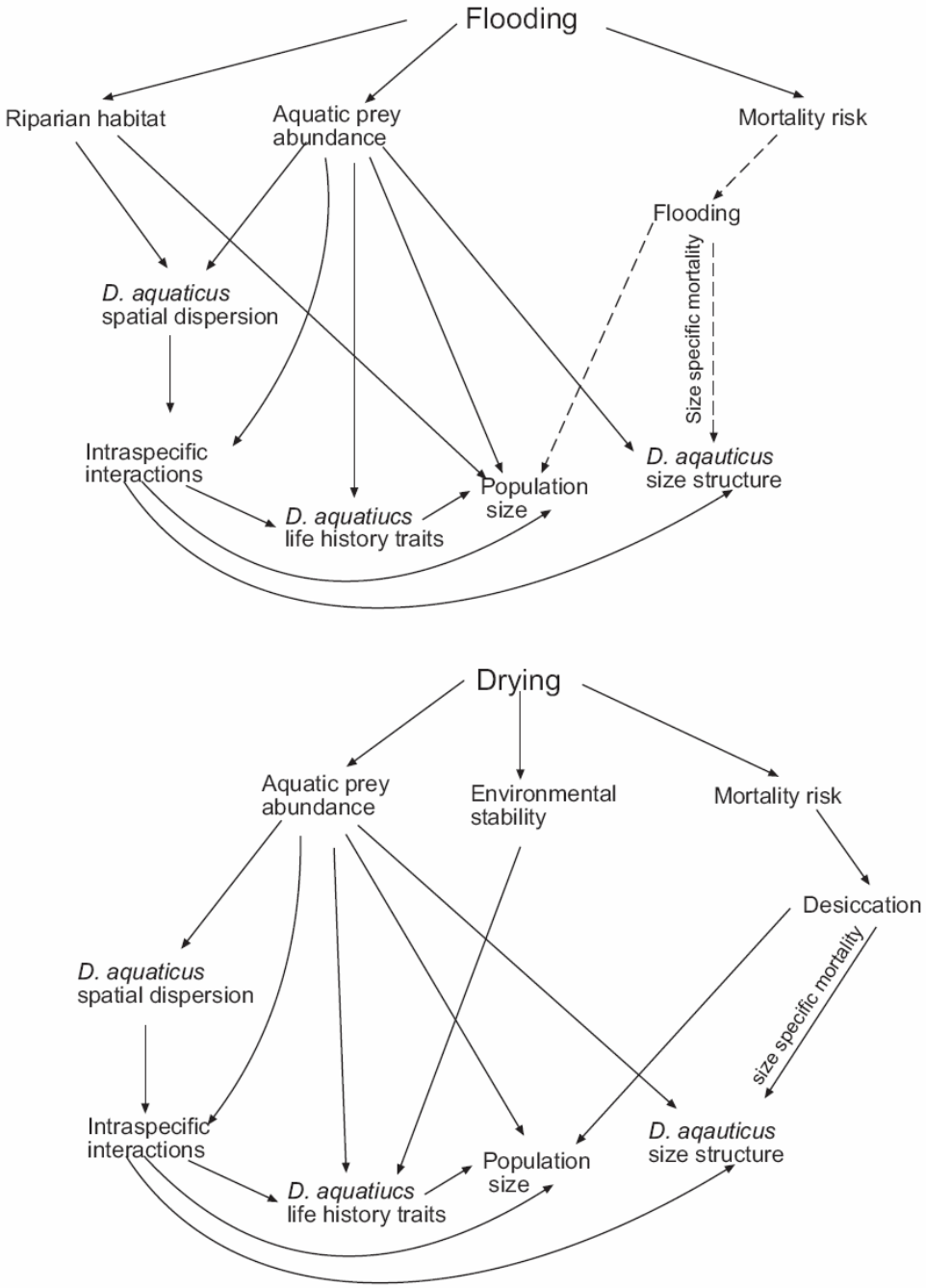

Figure 1 Summary diagrams of the impacts of flooding and drying flow regimes on populations of *D. aquaticus* through changes to habitat availability, aquatic prey abundance, environmental stability and mortality risks related to flow regime. Mortality impacts of flooding on *D. aquaticus* are only likely to occur in very large flood events, this is indicated by the dashed arrows. The relative impact of each factor varies depending on the specific flood or drying regime of the river (see Table 1).

Many other terrestrial predators that use exposed riverbank habitat and feed on aquatic insect prey, for example, other cursorial spiders and lizards, are likely to be affected by the same conditions as *D. aquaticus* and the model described above is likely to hold for them also, at least in rivers with unconstrained channels. However, the relative impact of predatory and competitive interactions with other species needs to be investigated further for specific taxa. The responses of individual species to prey subsidies will depend on the community structure at a particular site as the presence of other predatory taxa (Krupa and Sih 1998, Marczak et al. 2007b) and degree of food limitation (Power et al. 2004) can modify the foraging behaviour and feeding efficiency of consumers using cross-ecosystem subsidies. *D. aquaticus* is the largest terrestrial predatory arthropod inhabiting the riverbank habitat at my study sites and as such may have been competitively dominant and safe from intraguild predators (excluding conspecifics) once large size was reached. However, many other species in riparian food web are likely to be affected significantly by the presence of additional predatory species. Such interactions, as well as specific habitat requirements, prey preference and mobility (Power et al. 2004) of the focal taxa would need to be investigated to be able to predict their responses to variations in cross-ecosystem prey transfer.

Future research

Organisms that forage at ecosystem boundaries can have large effects on the amount of subsidy entering the recipient habitat, for example water striders consumed over 90% of terrestrial insects falling into isolated pool habitats (Marczak et al. 2007b) and predatory arthropods (spiders and beetles) ate over half of the aquatic insect biomass emerging from a braided river (Paetzold and Tockner 2005). Surface foraging predators act directly at the boundary consuming prey before it has the opportunity to reach other predators. These interactions mean the transfer of aquatic biomass to the terrestrial food web may be facilitated (i.e., the spiders get eaten by larger prey) or reduced (interception of prey at water surface) by *D. aquaticus. D. aquaticus* are unlikely to act as trophic ‘cul de sacs’ (sensu Power 2006), preventing aquatic resource from passing further up the food chain as they have the potential to be eaten by a range of predators including lizards and birds. How the magnitude of transfer of aquatic biomass via *D. aquaticus* to the terrestrial environment varies across

environmental gradients, such as those studied in this thesis, is an interesting question that merits further investigation.

Some of the predictions of relative impacts of the various factors described above are likely to be complicated if the nature of aquatic prey changes across flow regime gradients. The type of the aquatic insects present in a river has been shown to change across flood disturbance gradients overseas, altering their availability to predatory invertebrates and fish (Wootton et al. 1996, Marks et al. 2000). However, New Zealand rivers tend to contain a core of generalist taxa (Winterbourn et al. 1981) and across the environmental gradients studied here taxonomic composition of aquatic insect communities did not change substantially. Prey with non-terrestrial phases, e.g., snails, were not present in any of the study rivers in large numbers and potential aquatic prey biomass was estimated using only aquatic taxa with a terrestrial stage. The main differences were that fewer species and lower biomass were found at the more flood-prone and drier sites. Changes to the relative abundance of taxa with different emergence strategies as adults, e.g. taxa that crawl to the water edge or that emerge as adults from the water surface, may alter their availability to terrestrial predators (Paetzold et al. 2005). Furthermore, seasonal or yearly variation in flow regimes will affect river productivity and may lead to differences in the importance of aquatic insect prey to riparian predators (Takimoto et al. 2002, Power et al. 2004). Thus, changes in the abundance and nature of aquatic insects across environmental gradients both spatially and temporally must be incorporated into future investigations.

Implications of my research

In order to predict when subsidies of resources across ecosystem boundaries are likely to have significant impacts in the recipient system factors that control the magnitude of the subsidy, that constrain the consumers response to the subsidy and that influence the impact of the subsidised consumer in the food web need to be included (Polis et al. 1997, Power et al. 2004). The main influences of flow regime on factors within these categories are depicted in Figure 2 (see Table 2 for supporting references). This diagram summarises the multiple influences that changes in flow regime could have on the significance of aquatic insect subsidies for terrestrial food webs. The relative strengths of the linkages will vary depending on the specific consumer been investigated and the flow regime of the river.

Global change to climate patterns, the extent and continuity of habitats and the distribution of introduced species are likely to have large impacts on the nature and extent of subsidies between ecosystems (Riley and Jefferies 2004), as well as their impact in the recipient habitat by changing many of the factors illustrated in Figure 2. Such changes may alter the relative importance of factors constraining or facilitating predator responses to prey subsidies. For example, changes to river flow regimes, through climate change (Arnell et al. 1996), water abstraction and the presence of dams can all have strong effects on riparian predators of aquatic insects and not just by altering prey availability. For example, river flow patterns can alter the ability of surface-feeding predators to catch prey (Bleckmann and Barth 1984, Bleckmann et al. 1994, Marczak et al. 2007b). Moreover, if the physical structure of riparian zones changes then the suitability of an area as a habitat and foraging ground for many taxa will be modified (Greenwood et al. 1995, Ellis et al. 2001, Bonn et al. 2002, Ballinger et al. 2005), and the nature of linkages between the two systems will change. Many insectivorous birds prefer forested riparian zones as they provide cover and roost sites (Wiebe and Martin 1998) and bats may often prefer open river banks to forage over as their echolocation is not interfered with by turbulence from the water or by surrounding obstacles (in Power and Dietrich 2002). Many web spinning spiders are also dependent on riparian vegetation for web attachment and as I have shown, some cursorial spiders, and potentially lizards, depend on loose, riverbank rock habitat (Chapter Two). Thus, anthropogenic modifications to flood regimes will not only alter the nature and magnitude of aquatic insects emerging (Power et al. 1996, Lytle and Poff 2004, Paetzold 2004) but also the suite of terrestrial predators that feed on them and thus the pathway through which aquatic biomass enters the terrestrial food web (e.g. Paetzold et al. 2006).

The research presented in this thesis provides a model of interacting and limiting factors across a range of environmental conditions that modify population responses of one species to cross-ecosystem subsidies. It provides an initial step towards a predictive model of the conditions under which subsidies of prey may have large impacts on recipient communities. Such models will have to include factors that alter the magnitude of resource subsidy relative to autochthonous production, for example, the ratio between boundary length and recipient ecosystem area and the permeability of the boundary to resource flows, as well as the specific characteristics of the recipient communities that may alter responses to the subsidies, for example

feeding and habitat preferences of specific taxa and biotic interactions between them (e.g. Figure 2). One way to simplify this is to investigate the relative impacts of such processes across environmental gradients, as done in this thesis. In this way theoretical predictions can be developed and tested. In this example, ecosystem boundary length, the relative productivity of the aquatic and terrestrial ecosystems, boundary permeability to aquatic insect dispersal, the identity of emerging aquatic insects and the community composition of terrestrial predators of aquatic prey are likely to vary in predictable patterns across river flow regime gradients and the relative importance of each process can be experimentally tested in a variety of environmental conditions. The next step will be expanding these ideas from a single species study to encompass community dynamics in response to cross–ecosystem subsidies. Such a process becomes complex when dealing with species-specific feeding and habitat preferences and dispersal scales (e.g. Power et al. 2004) but a useful approach could be trait-based with potential consumers of the prey subsidy combined into feeding preference or habitat type categories.

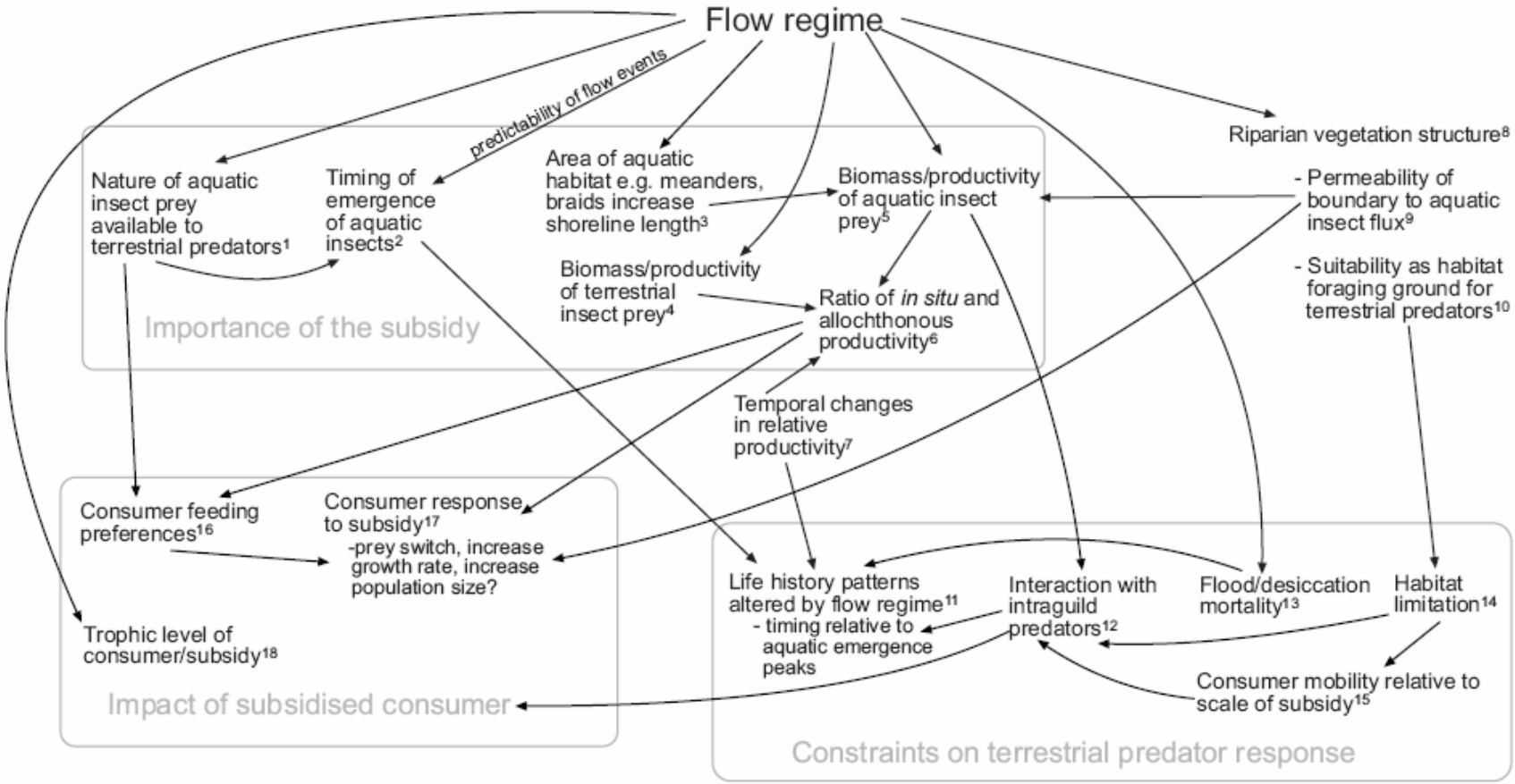

Figure 2 Theoretical diagram showing the main effects of river flow regime on the magnitude of aquatic insect subsidies to terrestrial consumers, on constraints to the consumers response to the subsidy and the impact that the subsidised consumer has in both the terrestrial and aquatic food-webs. The relative importance of each factor will vary depending on the flow regime of the river. Superscript numbers refer to relevant references (see Table 2).

Table 2 Supporting references for Figure 2. Numbers correspond to links in the flow diagram.

	No.		Reference
Magnitude / importance of the subsidy	1	The identity of aquatic insects changes their availability as prey to terrestrial predators	Aquatic prey, aquatic predators: Wotton et al. 1996, Marks et al 2000.
	2	Flow regime alters the timing of aquatic insect emergence, depending on predictability of the disturbance	Floods; Lytle 2001, Lytle and Poff 2004. Water temperature; Harper and Peckarsky 2006.
	3	Increased boundary length increases subsidy levels to recipient habitat	Polis and Hurd 1995, Polis et al. 1997, Cadenasso et al. 2004, Witman et al. 2004. Meanders increase aquatic insect abundance in riparian forest; Iwata 2003.
	4	Biomass/productivity of terrestrial insects affected by flow regime	Chapters 2 & 5, Flooding; Bonn et al. 2002, Ellis et al. 2001.
	5	Biomass/productivity of aquatic insect prey altered by flow regime	Chapters 2 & 5, Gray 1993, Whiles and Goldowitz 2001, Chadwick and Huryn 2007.
	6	Ratio of terrestrial to aquatic productivity determines importance of subsidy to consumer	Persson et al. 1996, Polis et al. 1997, Nakano et al. 1999, Marczak and Richardson 2007, Marczak et al. 2007.
	7	Temporal changes in relative productivity of systems	Nakano and Murakami 2000, Takimoto et al 2002, Marczak et al. 2007.
	8	Flow regime can alter riparian vegetation structure	Flooding; Bendix 1997.
	9	Permeability of ecosystem boundary to aquatic prey flux	Delettre and Morvan 2000, Cadenasso et al. 2004, Witman et al 2004.
	10	Riparian habitat suitability for terrestrial predators changed by river flow regime	Chapter 2, Greenwood et al. 1995, Ellis et al. 2001, Bonn et al. 2002, Ballinger et al. 2005.
	11	Life history patterns of terrestrial consumers altered by flood regime	Chapter 4, timing of life history in relation to peak

			prey abundance, Ostfeld and Keesing 2000, Paetzold et al. 2006
Constraints on consumer response	12	Interactions (predation and competition) with other intraguild predators alters consumers response to subsidy and effect in food web	Chapter 3, Polis and Hurd 1995, Krupa and Sih 1998, Stapp and Polis 2003.
	13	Consumer may be susceptible to flood mortality/desiccation risk	Chapter 2 & 5, De Vito et al. 2004.
	14	Terrestrial predator may be habitat limited	Chapter 2.
	15	Consumer mobility/dispersal ability relative to scale of subsidy	Power et al. 2004.
Impact of consumer in recipient food web	16	Consumer feeding preferences, specialist or generalist	Polis et al 1997, Power et al. 2004, Paetzold and Tockner 2005.
	17	Consumer response to subsidy, prey switch or increase in abundance or growth rates	Baxter et al 2005.
	18	Trophic level of subsidy and consumer	Polis et al. 1997, Huxel et al 2002, Anderson and Polis 2004.

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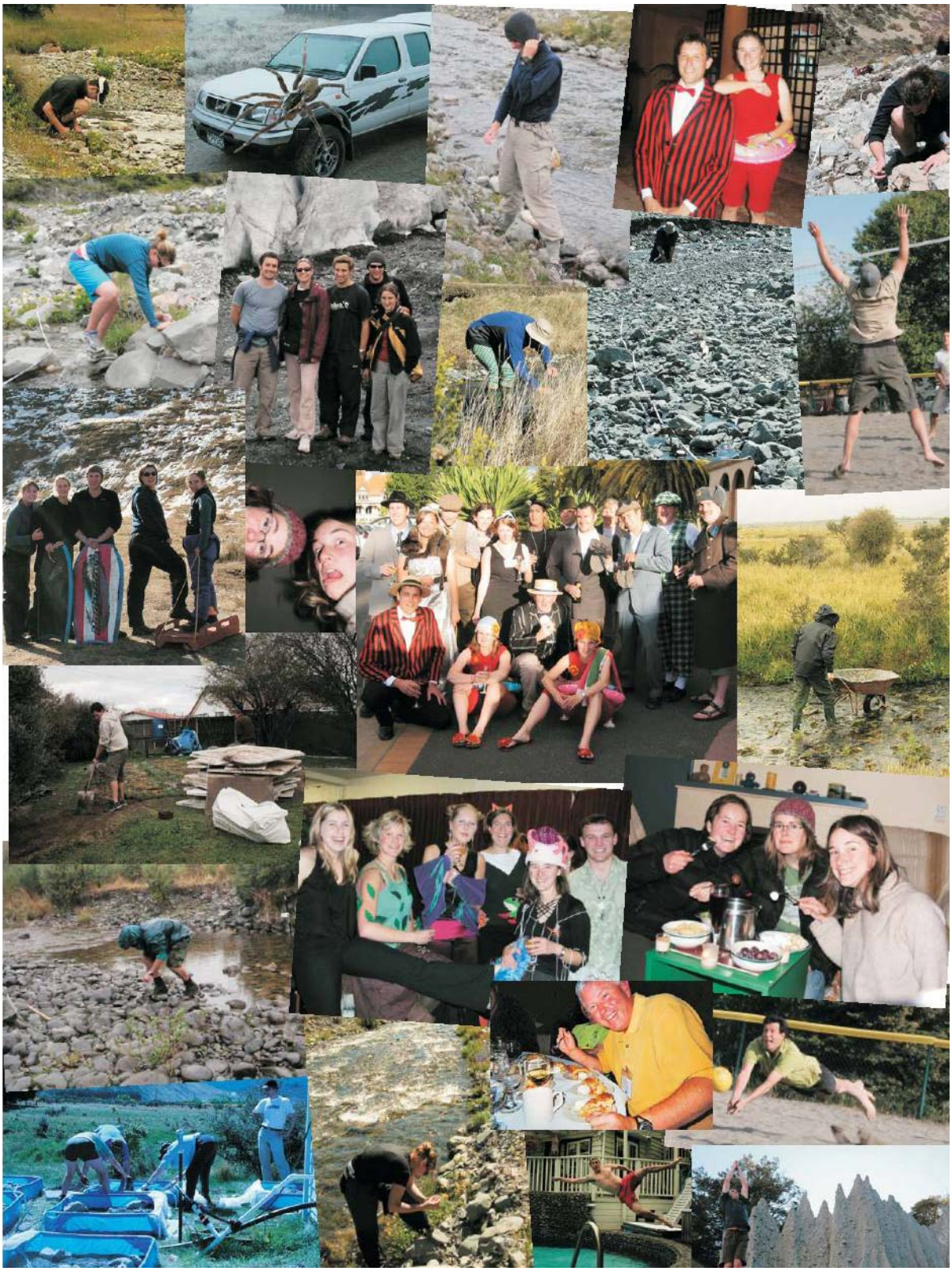

Appendix I Physical characteristics of the flood disturbance gradient study rivers in Chapters 2, 3, and 4. A high river disturbance index (RDI) score (Pfankuch 1975) indicates a river more disturbed by floods. Grid references refer to Infomap 260 published by the Department of Survey and Land Information, New Zealand.

River	Grid ref.	RDI	Mean (± 1SE) proportion tracer rocks moved in 12 months	Mean (± 1SE) bank substrate size (mm)	Proportion of 600 m of bank covered by >5% vegetation	River width (m)
Porter River†	K34:065728	60	0.03 (0.01)	108 (6)	0.44	8.2
Dry Stream	K34:055714	82	0.12 (0.05)	88 (5)	0.21	2.1
Thomas River	K34:056776	65	0.14 (0.03)	75 (6)	0.44	1.9
Coralyn Spring*†	K34:036972	53	0.0	95 (10)	0.58	8.2
Broken River†	K34:070783	60	0.04 (0.01)	107 (7)	0.22	6.5
Cave Stream†	K34:064801	52	0.01 (0.01)	93 (5)	0.83	3.0
Craigieburn‡	K34:085845	55	0.2 (0.01)	112 (11)	0.93	5.0
Waimakariri River	K34:075994	110	0.6 (0.11)	74 (7)	0.0	20.0
Ribbonwood Stream	K34:102910	91	0.36 (0.09)	68 (5)	0.0	2.1
Cass River	K34:079970	67	0.3 (0.05)	63 (5)	0.01	4.1
RJ Spring*†	L34:134979	50	0.0	71 (4)	0.72	1.9
Broad Stream	K34:003964	99	0.35 (0.10)	82 (7)	0.0	2.8
Bruce Stream	K34:985966	99	0.47 (0.09)	92 (8)	0.0	5.9

* unofficial name

† used in habitat manipulation experiment

‡ not used in Chapters 3 and 4 as too few spiders

Appendix II Site photos of 13 rivers used in the flood disturbance gradient in Chapters 2, 3 and 4. Sites are generally ordered from stable to highly flood disturbed.

RJ Spring

Cragieburn

Cave Stream

CoralynSpring

Porter River

Broken River

Cass River

Thomas River

Dry Stream

Ribbonwood Stream

Broad Stream

Bruce Stream

Waimakariri River